

CONTRIBUTIONS TO PALAEONTOLOGY
FROM CARNEGIE INSTITUTION OF WASHINGTON

STUDIES OF THE
PLIOCENE PALAEOBOTANY OF CALIFORNIA



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LIST OF PAPERS

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- II. Woods from the Ricardo Pliocene of Last Chance Gulch, California. By Irma E. Webber. Pages 113 to 134, 5 plates.

I
PLIOCENE FLORAS OF CALIFORNIA

By ERLING DORF

With thirteen plates and one text-figure.

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PLIOCENE FLORAS OF CALIFORNIA

INTRODUCTION

It is the purpose of this paper to describe fossil plant remains from the Pliocene deposits of California and to discuss as fully as possible the physical and environmental conditions under which they lived, as well as their stratigraphic significance. The plant remains are nowhere abundant nor are they as perfectly preserved as might have been wished. The small collections which have been made, however, have resulted in the recognition of thirty-four species, the associations of which, at sixteen localities, are consistently indicative of the same general climatic conditions. It is hoped that the present paper will contribute materially toward filling in the gap which has long existed in the Tertiary plant record of western North America between the Miocene and Pleistocene epochs.

The study of the Pliocene floras was begun in the summer of 1927, at the suggestion of Dr. R. W. Chaney of the Carnegie Institution of Washington. A good collection was secured at that time from the Sonoma tuffs. During the following summer additional material was collected from new localities in the Wildcat formation, the Sonoma tuffs, the Merced sandstones, and the Pico shales. A collection of plants which Dr. Chaney had collected some years previously was also secured, and abundant remains were collected from the Santa Clara beds, from which Hannibal had previously described¹ a small flora. During this summer the writer was assisted by H. L. Mason and S. Dorf. The summer of 1929 yielded good collections from new localities in the Orinda and Etchegoin formations and from a new horizon of the Sonoma tuffs. Valuable material from Alturas was also obtained from Dr. Chaney, and cone material from the Merced sandstone was secured from H. L. Mason. The entire project has been done under the auspices of Carnegie Institution of Washington and Princeton University.

A number of references to the presence of fragmentary plant remains in the Pliocene deposits of California have been published by various authors, notably Merriam,² Lawson,³ and Nomland.⁴ None of these occurrences, however, seems to have furnished material sufficiently abundant or well-preserved to make accurate de-

¹ Hannibal, Bull. Torrey Bot. Club, vol. 38, 329, 1911.

² Merriam, Univ. Calif. Dept. Geol. Bull., vol. 7, No. 19, 383, 1913.

³ Lawson, U. S. Geol. Surv., 15th Ann. Rpt., 460, 1895.

⁴ Nomland, Univ. Calif. Dept. Geol. Bull., vol. 9, No. 6, 79, 1916.

terminations possible. The first scientific paper, as far as the writer is aware, to be devoted mainly to the discussion of Pliocene plant materials is by Marsh, on *A Fossil Forest in the Tertiary of California*,¹ in which he describes the occurrence of petrified logs in the Somona tuffs near Calistoga. The wood is here referred to *Sequoia* by M. C. White and the tuffs are described as of probable Pliocene age. A more comprehensive description of silicified wood from the same locality was subsequently published by Platen,² in 1907. By far the most important contribution to Paleobotany has been *A Pliocene Flora from the Coast Ranges of California*, by Hannibal,³ in which he describes plant material from the Santa Clara beds of the region south of San Francisco Bay. A tentative revision of Hannibal's collections, in which all the forms were referred to modern species, was recently made by Chaney.⁴ On the basis of the writer's collections from the Santa Clara beds and a study of Hannibal's type specimens at Leland Stanford Junior University a more complete revision will be attempted in the present paper.

Other Pliocene material has furnished comments and inferences to Chaney's recent paper on the Mascall flora.⁵ Another recent report on Tertiary conifers of western America, by Mason,⁶ describes the occurrence of coniferous material at two Pliocene localities. Both Chaney's and Mason's material is included in the present report.

No other references have been made to Pliocene plant remains other than mere incidental mention of fragmentary material in scattered localities throughout the state.

The stratigraphic and structural relations of the Pliocene formation of California have been adequately treated in numerous publications which will be mentioned in the detailed descriptions of the various formations from which fossil plants have been collected.

The writer takes this opportunity to express his appreciation to Carnegie Institution of Washington and the Department of Geology of Princeton University for their support of the project, and to the Department of Geology of the University of Chicago, in whose laboratories the work was completed. It is a pleasure to acknowledge the cooperation and encouragement rendered by Dr. R. W. Chaney of Carnegie Institution, under whose direction the work has been done, and who has given invaluable assistance in the final completion of the manuscript. Other helpful suggestions have been received from Mr. H. L. Mason, of the University of California, Dr. Arthur Hollick, of The New York Botanical Garden, Dr. A. C. Noé, of the University

¹ Marsh, Amer. Jour. Sci. and Arts, 3d ser., vol. 1, 266, 1871.

² Platen, Natur-Forsch. Gesell. zu Leipzig, vol. 34, 4, 1907.

³ Hannibal, Bull. Torrey Bot. Club, vol. 38, 329-343, 1911.

⁴ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 45, 1925.

⁵ Chaney, op. cit., 25-48.

⁶ Mason, Carnegie Inst. Wash. Pub. No. 346, pt. V, 138-158, 1927.

of Chicago, and Dr. Paul C. Standley, of the Field Museum, Chicago. For the use of herbarium materials the writer is grateful to The New York Botanical Garden, the Field Museum, and the University of California. Material aid has been received from Dr. A. F. Buddington, of Princeton University, in the petrographic examination of sediments.

GEOGRAPHIC DISTRIBUTION OF PLANT LOCALITIES

The localities from which Pliocene plant remains have been obtained center about the San Francisco Bay Region of California. The accompanying map (plate 1) indicates the distribution of the plant-bearing outcrops by groups rather than by single localities, as many of the locations are in such close proximity as to make it impracticable to attempt to represent each one by a circle.

Ten of the localities are situated less than 35 miles from San Francisco Bay. To the north, five localities in the Sonoma formation and one in the Merced, represented by circles 1 and 2 respectively, lie just east of the Santa Rosa Valley in the eastern portion of Sonoma County and the western border of Napa County. To the east of the bay, two localities in the Orinda, at circle 3, lie in the Berkeley Hills of Contra Costa County. To the south, one locality in the Merced formation, represented by circle 4, lies directly on the coast near the boundary between San Francisco and San Mateo Counties, and one locality, at circle 5, lies in the Santa Clara valley, in the eastern portion of Santa Clara County.

The remaining six localities are situated at considerable distances from San Francisco Bay, four to the north and two to the south. Three localities at circle 6 lie in the southern portion of Humboldt County, in the valley of the south fork of the Eel River, and one locality at circle 7 is in Modoc County near the western margin of the Warner Mountains in the Pitt River valley. In the southern part of the state the locality represented by circle 8 lies in the southwestern part of King County, and the locality at circle 9 lies directly on the coast in the southwestern section of Ventura County.

Physiographically the sixteen localities may be grouped as follows:

Coastal.....	④—Locality 159.
	⑨—Locality 161.
Outer Coast Ranges and Valleys.....	①—Localities 150,151,152,153,154.
	②—Locality 158.
Inner Coast Ranges and Valleys.....	③—Localities 162, 163.
	⑤—Locality 160.
	⑥—Localities 155, 156, 157.
Great Valley.....	⑧—Locality 164.
Interior Ranges.....	⑦—Locality 165.

STRATIGRAPHIC OCCURRENCE OF THE FLORAS

Table 1, based mainly on Clark's recent correlation table¹ and accompanying text, indicates the stratigraphic occurrence of the plant-bearing horizons in the Pliocene formations of California. The column for the Sonoma formation, which is not shown in Clark's table, is based on recent reports by Dickerson² and Lawson.³ The Alturas formation, concerning which very little has been published, is placed in the upper Pliocene on the basis of its stratigraphic relations and its vertebrate fauna.⁴

TABLE 1

GEOLOGICAL TIME SCALE	COUNTIES							
	HUMBOLDT	SONOMA AND NAPA	CONTRA COSTA	SAN MATEO	SANTA CLARA	KING	VENTURA	MODOC
PLEISTOCENE							LOS POSAS	
UPPER PLIOCENE			BERKELEY GROUP		SANTA CLARA	TULARE	SANTA BARBARA	ALTURAS
MIDDLE PLIOCENE	WILDCAT	SONOMA	ORINDA	MERCED	PURISSIMA	ETCHEGOIN	PICO	
LOWER PLIOCENE		MERCED	PINOLE			JACALITOS		

▬▬▬ PLANT-BEARING HORIZON

It is evident that most of the formations are of lower to middle Pliocene age. While it is impossible to prove that any one of the floras is strictly contemporaneous with any of the others, the later consideration of the individual floras clearly reflects the general uniformity of conditions during each of the various portions of the Pliocene epoch and is in general accord with the age relations as indicated.

In the discussion which follows, the occurrence of the plant-bearing horizons within each of the various formations is treated in detail. The formations are considered in the order of (1) their age-relations, *i. e.* lower Pliocene to upper Pliocene; (2) their importance, based on size of collections and number of localities in each; (3) their geographic location.

¹ Clark, *Stratigraphy and Faunal Horizons of the Coast Ranges of California*, 1929.

² Dickerson, *Cal. Acad. Sci.*, 4th ser., vol. XI, No. 19, 527, 1922.

³ Lawson, *U. S. Geol. Surv.*, San Francisco Folio, 13, 1914.

⁴ Stock, Oral communication, Dec. 14, 1929.



Map of California, indicating location of Pliocene localities from which fossil plants have been collected.

SONOMA FORMATION

Five leaf localities have been discovered in the Sonoma tuffs in the vicinity of Santa Rosa. These will be discussed separately below.

The Sonoma tuffs constitute one phase of the Sonoma group¹ of basalts, rhyolites and tuffs, which extends over a large portion of Napa County, overlapping into the eastern portion of Sonoma County, and the southern portion of Lake County. At their western border both the basalts and tuffs of the Sonoma group are intercalated in the lower portion of the Merced sandstones.² Although generally regarded as of middle Pliocene age, the lower portion of the Merced is probably the correlative of the Jacalitos formation of lower Pliocene age.³ Lower Merced invertebrates have been found by Dickerson in both the sandy and tufaceous portions of the intercalated series. It is significant that three leaf localities, two in the tuffs and one in the sandstones, occur along the line of the interfingering of the continental and marine sediments which evidently took place along the shoreline of the Merced embayment.

Both the Sonoma volcanics and the Merced sandstones overlie unconformably the Franciscan series of Jurassic age and, more locally, the Petaluma lake beds of upper Miocene age.

The Sonoma tuffs are areally connected with the Pinole tuffs of the Berkeley Hills and have been found intercalated with the Orinda formation of the same region.⁴ It may thus be seen that in addition to its correlation with the lower Merced, the Sonoma group may also be regarded as the stratigraphic equivalent of the Pinole-Orinda series, which is likewise referred to the lower Pliocene.

Based on the discovery of the horse remains, *Neohipparion gidleyi* Merriam,⁵ in beds intimately associated with the basalts and tuffs of Sonoma Mountain⁶ the Sonoma group has been correlated with the Orinda of the Berkeley Hills and the Jacalitos of the San Joaquin Valley.

Two of the plant localities occur in the vicinity of "The Petrified Forest," situated five miles west of Calistoga and about ten miles northeast of Santa Rosa. The numerous petrified trunks at this location have for many years attracted scientific as well as popular interest. As far back as 1870 the region was visited by Professor O. C. Marsh of Yale, who in the succeeding year published a short

¹ Osmont, Univ. Calif. Dept. Geol. Bull., vol 4, No. 3, 58, 1904.

² Dickerson, Cal. Acad. Sci., 4th ser., vol. 11, No. 19, 556, 1922.

³ Clark, Oral communication, Sept. 12, 1929.

⁴ Lawson, Oral communication, Sept. 1927.

⁵ Merriam, Univ. Calif. Dept. Geol. Bull., vol. 9, No. 1, 1, 1915.

⁶ Dickerson, Cal. Acad. Sci., 4th ser., vol. 11, No. 19, 553, 1922.

account¹ of the occurrence in which he ascribes its discovery to Charles E. Denison, who had previously written a short article concerning it for the San Francisco Bulletin. Extensive excavation of the prostrate logs was begun in 1871 by Mr. C. Evans and later continued by Mr. and Mrs. D. G. Bockée, resulting in the exposure of a great number of beautifully preserved logs. A more detailed description of the occurrence was subsequently published by Dickerson.²

The presence of fossil leaves in the tuffs was noted only recently by Mrs. D. G. Bockée, the present owner and operator of "The Petrified Forest," in the excavation of one of the larger trunks. The writer's attention was called to the occurrence by Dr. R. W. Chaney, resulting in the discovery of an additional number of leaf horizons in the near vicinity.

The observed section in the region consists of a basement of highly metamorphosed Franciscan rocks overlain unconformably by the alternating series of basalts, rhyolites and tuffs of the Sonoma group, dipping at an angle of 12° to 30° toward the north and striking approximately east and west. The Franciscan rocks are exposed in the ridge a half mile south of the Bockée residence, and are apparently highly metamorphosed basalts. In all of the region north of this Franciscan core the country rock consists of the Sonoma group of massive, conglomeratic, sandy tuffs and tuff breccias interbedded with thinner layers of basaltic and rhyolitic extrusives, which form the capping of several of the numerous ridges.

LOCALITY 150

This is the principal locality near "The Petrified Forest," having furnished the largest number of species as well as of individual leaf specimens. It is situated along the fire trail which runs along the southern slope of a ridge a third of a mile slightly north of west from the Bockée residence. The best material was collected from a two-foot ledge of fine-grained volcanic ash directly in the trail and 100 yards from where it begins at the base of the slope. This same horizon, followed laterally up the trail, yielded a smaller collection at a point 200 feet from the first location. Bedding planes are lacking in the rock and the leaves are irregularly scattered and variously curled and twisted, suggesting subaerial deposition.

The matrix in which the leaves occur is a white or grayish-white volcanic ash, made up wholly of volcanic material in which are intermingled numerous fragments of pumice. It has been examined petrographically by Dr. A. F. Buddington of Princeton University and is seen to be a silicified volcanic, vitro-clastic dust containing typical

¹ Marsh, Amer. Jour. Sci. and Arts., 3d ser., vol. 1, 266, 1871.

² Dickerson, Cal. Acad. Sci., 4th ser., vol. 11, No. 19, 555, 1922.

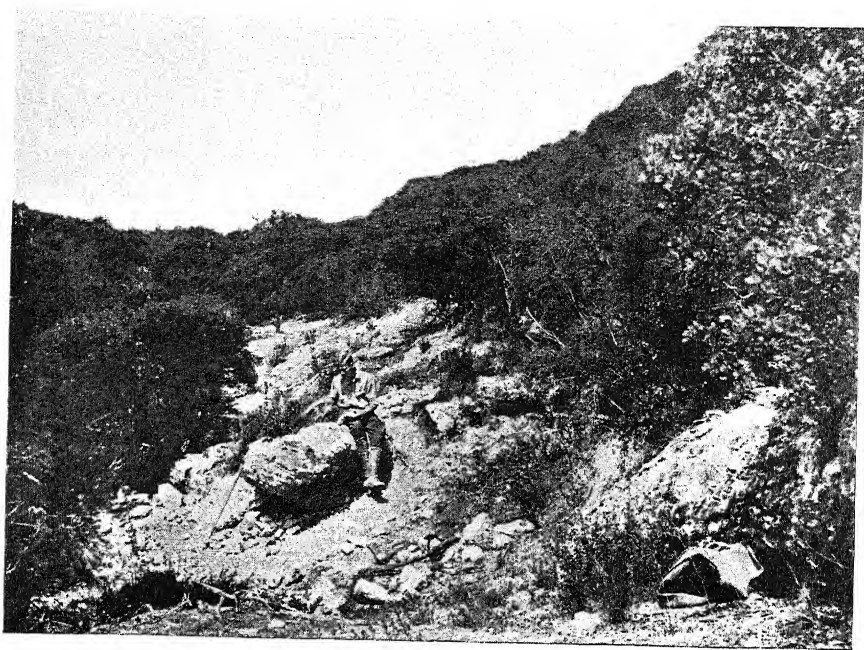


FIG. 1—Plant Locality 150, near "The Petrified Forest," California, showing exposure of Sonoma tuffs on chaparral covered slope. Plant horizon occurs in cut in lower left center of picture.

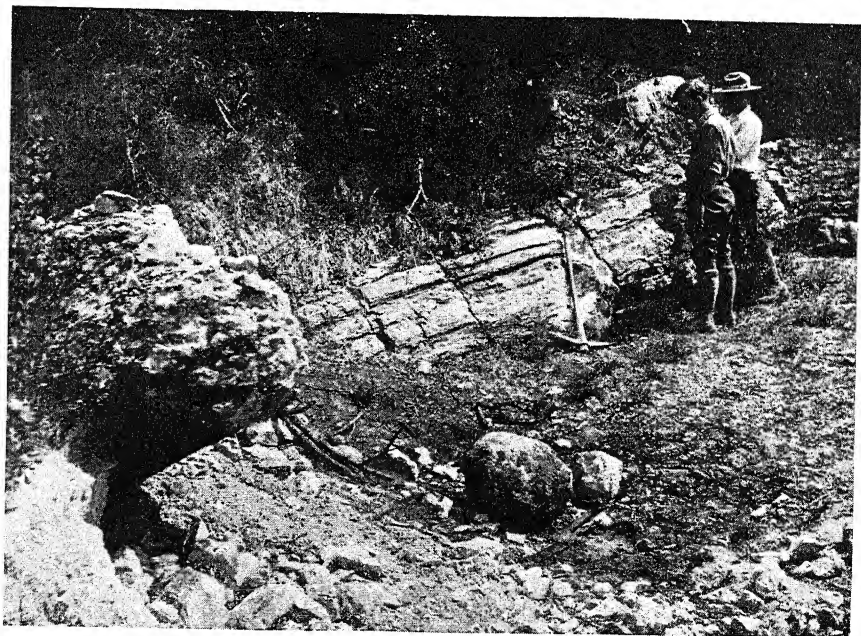


FIG. 2—Another view of Locality 150, showing occurrence of petrified logs along slope of hill. Tuff in lower left-hand corner contains leaf impressions.

glass shards or "bows," numerous crystals of clear plagioclase and scattering fragments of micro-crystalline lava. No trace of quartz or orthoclase was seen in the sections. The unbroken condition of the "bows" suggests deposition on land or in standing water. The latter, however, would hardly result in the preservation of the leaves in such a curled and twisted condition, rather giving rise to flat preservation along bedding planes. The evidence of both the condition of the leaves and the nature of the tuff therefore suggests sub-aerial conditions of deposition with little or no transportation by water.

A small collection of leaves, mostly of conifers, and of excellent cone material was made from a lense of slightly coarser ash 50 feet higher than and slightly to the east of the above locality. The ash is exposed at the base of a four-foot ledge and lies directly below a lenticular mass of conglomerate. It is probable that at least the ash in which the plant material is entombed was deposited subaerially, as a number of open fir cones were encountered, which would undoubtedly have closed tightly, as do their living counterparts, when immersed in water.

Petrified wood is common along the slopes of the ridge and occasionally may be represented by complete trunks protruding from the surface of the hill. Four of such trunks are exposed 2 feet stratigraphically above and 10 feet east of the first locality mentioned. The lowermost is 5 feet in diameter, runs approximately east and west, and is exposed for a horizontal distance of 25 feet; the remaining three are somewhat smaller in diameter, point in a north-south direction, and are exposed for only a foot or so directly above the first trunk.

In spite of the fact that over 600 individual leaf specimens have been examined at this locality, the number of species is rather small. In the following lists, the species are arranged according to their order of dominance in each of the horizons.

Lower horizon:

Quercus bockéi
Ilex sonomensis
Umbellularia oregonensis
Sequoia langsdorffii
Pseudotsuga sonomensis
Odotemon hollicki
Heteromeles sp.
Smilax sp.

Upper horizon:

Sequoia langsdorffii
Pseudotsuga sonomensis
Quercus lakevillensis
Umbellularia oregonensis

LOCALITY 151

Two leaf horizons occur within the actual limits of "The Petrified Forest," which is situated on the slope just north of the Bockée residence. The first is in the east wall of the tunnel running into the hill along the "Monarch," or "Tunnel Tree," and is about 15 feet

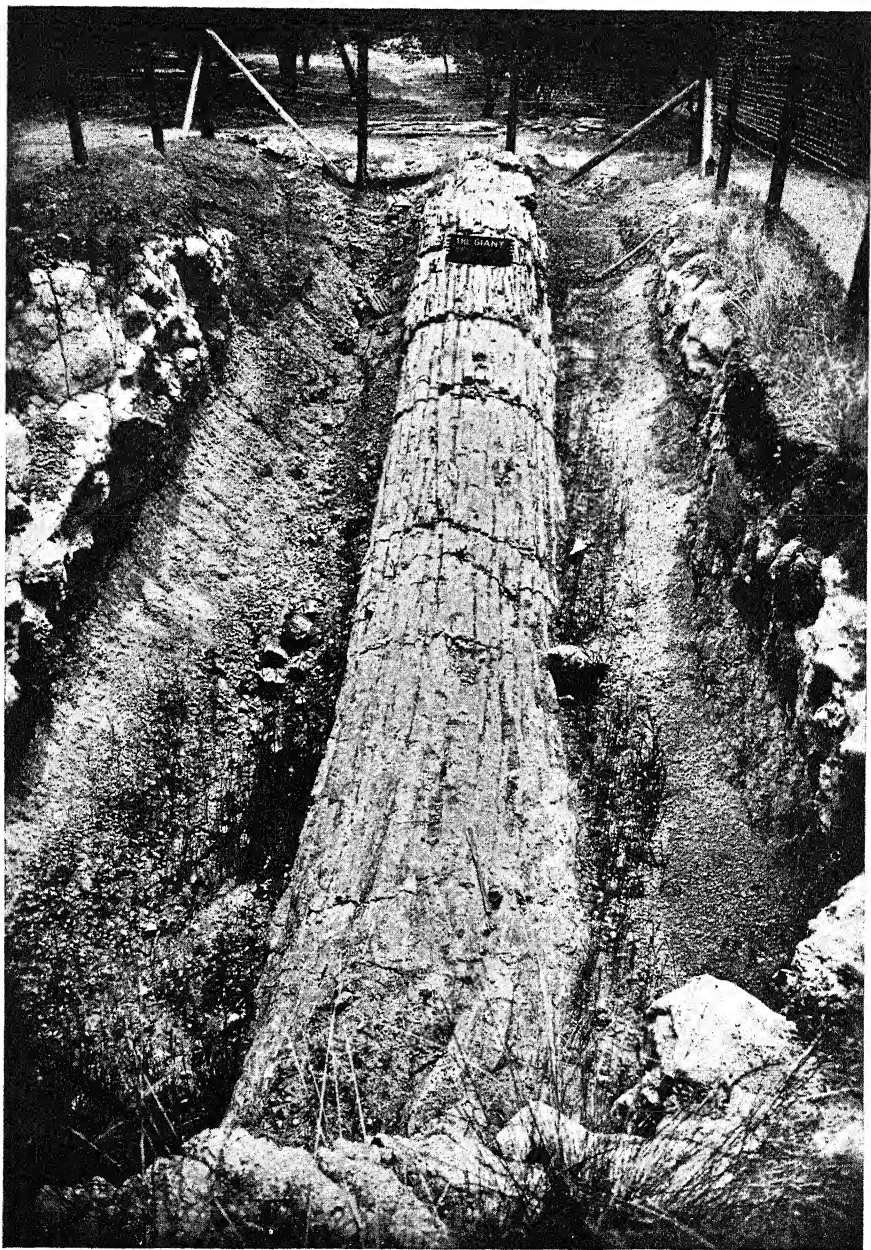
from the entrance of the tunnel and a few inches above the level of the floor. It was discovered by Mrs. D. G. Bockée during the process of tunneling. The enclosing matrix is a greenish-gray, altered, volcanic ash in which the leaves have been only poorly preserved. A petrographic examination by Dr. A. F. Buddington indicates that it is an altered, micro-crystalline, glassy tuff, with the plagioclase crystals unaltered, suggesting a bentonitic character. This is strengthened by the fact that it swells and disintegrates on immersion in water.

The second horizon is situated in an excavated trench running along the eastern side of an unnamed trunk, 80 feet east of the "Monarch." The leaf impressions occur in a shattered, buff-colored, unaltered ash in both walls of the ditch, 1.5 feet below the surface.

The number of beautifully preserved petrified trunks on this slope is in striking contrast to the paucity of leaf impressions. Most of the larger trunks have been uncovered of their overburden of ash and exposed more or less completely to view by the present owners of the property. All of the trunks are prostrate and dip uniformly with the beds at an angle of 5° to 13° northward. Most of the trunks are oriented in the same general northeast-southwest direction, with the tops toward the southwest. The average seems to lie between north 35° east and north 45° east, with a lesser number directly north-south or a few degrees west of north. Dickerson has postulated¹ that this uniform direction is evidence that the "volcanic mud and pumice came in a great volume from the northeast." It is possible that the natural fall of trees on a southwest-facing slope might produce the same effect, regardless of the actual direction from which the ash was derived. In this connection it is significant to note that at locality 150, trunks were observed whose direction was almost directly east-west, while others at the same locality pointed north and south, perhaps indicating conditions in which the slope was more gentle and had, as a consequence, less influence on the direction of tree fall.

It was noted that the trunks at "The Petrified Forest" do not occur at the same elevation, but are separated by as much as 20 feet of vertical distance. It is possible that minor fault displacements may have separated horizons once contiguous. Another explanation might be that the trees of successively higher levels on a slope were entombed by a succession of different outbursts of volcanic material. This seems to be substantiated by the heterogeneity of the matrix surrounding the different petrified trunks, which would tend toward a more uniform lithology if the trees had all been covered by a single volcanic outburst.

¹ Dickerson, Cal. Acad. Sci., 4th ser., vol. 11, No. 19, 556, 1922.



View of "The Giant," one of the better preserved petrified trunks at "The Petrified Forest," near Locality 151. Removal of enclosing tuff has exposed trunk to a length of about 80 feet and diameter of 7 feet. (Photo through courtesy of Mrs. D. G. Bockée, present owner of property.)

One of the largest and most perfect trunks on the slope is the "Monarch" or "Tunnel Tree" mentioned above. A tunnel has been dug along its eastern side in order to expose as much as possible of the tree. About 125 feet have already been exposed, of which 30 feet are outside the entrance to the tunnel, and it is estimated that it may run at least 100 feet farther into the hill. It dips from 5° to 8° northward and lies north 45° east, with the top toward the southwest. The diameter, including the well-preserved bark, is about 5 feet at the top to 8 feet at the basal portion. The enclosing matrix is a rather coarse, gray to buff-colored ash, overlain by 20 to 25 feet, to the top of the slope, of finer, more firmly cemented ash. The entire length of the trunk is marked by uniformly spaced transverse cracks, though these are less distinct in this specimen than in most of the smaller trunks. These were undoubtedly produced by local movements or regional tilting of the beds subsequent to the silicification of the trunks. A microscopic examination of the wood has been made by Mrs. Irma Webber, of the University of California, who has referred it to the living *Sequoia sempervirens*, in which there is considerable variation in diagnostic characteristics.

It is to be regretted that leaf horizons are not more common at "The Petrified Forest" and that those which do occur are not well exposed; nor are the leaf impressions well preserved or numerous. The following species, which are of the same character at both horizons, indicate a rather pure growth of *Sequoia* and a few of its associates. The species are, as above, listed in their order of dominance: *Sequoia langsdorfi*, *Umbellularia oregonensis*, *Quercus lakevillensis*.

A comparison of the species encountered here with those found at locality 150 indicates a close resemblance to the association found at the upper horizon at that locality.

In view of the small number of leaf species represented in the Sonoma tuffs at this locality, mention should be made of previously recorded species based on wood determinations. The genus *Sequoia* was already reported in 1871 by M. C. White.¹ Besides *Sequoia*, Platen subsequently described two new species of oak (*Quercinium abromeiti* Plat. and *Q. lesquereuxi* Plat.), one pine (*Pityoxylon annulatum* Plat.), and an elm (*Ulmoxylon simrothi* Plat.).² The *Sequoia* and both of the oaks have equivalent leaf species in the Sonoma tuffs in the vicinity of "The Petrified Forest." No cones or leaf impressions referable to pine or elm have been discovered, although elm leaves occur in the Orinda formation of approximately the same age in the hills east of Berkeley, and pine cones have been found in the Merced sandstone of the same age a few miles south

¹ Marsh, Amer. Jour. Sci. and Arts, 3d ser., vol. 1, 268, 1871.

² Platen, Natur-Forsch. Gesell. zu Leipzig, vol. 34, 4, 1907.

of San Francisco. It is possible that remains of both these genera would have been encountered in the Sonoma tuffs if more extensive collecting had been possible.

LOCALITY 152

A number of leaf impressions have been collected by Dr. R. W. Chaney from the Sonoma tuffs exposed in the walls of Matanzas Creek, three miles southeast of Santa Rosa and 0.375 of a mile north-east of the Santa Rosa School, which is situated near the head of Bennett Valley. The locality is on the ranch of Mr. C. Bruggemann and lies in the south-central portion of Section 29, Range 7 west, Township 7 north, exactly 4.25 miles southeast of locality 154.

This locality has been visited during two successive summers by the writer, but only a few fragmentary leaf impressions were collected to add to the better impressions previously collected by Dr. Chaney. The observed section consists of the normal alternating layers of tuffs, sandstones, basalts and volcanic agglomerates of the Sonoma and Merced formations. The floor of the creek is made up of a basaltic conglomerate containing numerous scoriaceous pebbles, which is overlain by a white to cream-colored, sandy tuff, containing abundant plant remains, including both leaf impressions and a layer of petrified roots and stems.

Although the section is obscured by vegetal and soil covering it seems apparent that we are here concerned with the alternation of marine sandstones and continental volcanics as is observed elsewhere along the line of the Merced shore. The presence of ash, conglomerates and tufaceous mud-balls in the sandy sediments suggests deposition of the volcanic material along coastal streams or their debouchures into shallow marine embayments.

Seven species have been collected from this locality, arranged here according to their order of dominance:

Platanus paucidentata
Populus alexanderi
Populus prefrementii
Alnus merriami

Quercus declinata
Castanopsis chrysophylloides
Garrya masoni

LOCALITY 153

A very limited collection of plant remains from the Sonoma tuffs of Taylor Mountain, east of Bennett Valley, has been made by Dr. Chaney. The tuffs are exposed below a basalt flow on both the western and eastern flanks of the mountain. Plant impressions and scattered petrified wood occur in the ravines near the summit, exactly 1.75 miles west 50° south of locality 152 on Matanzas Creek.

Only three specimens, representing three species, have been collected from this locality: *Sequoia langsdorffii*, *Quercus lakevillensis* and *Woodwardia bennetti*.

LOCALITY 154

A good collection of fossil leaves was obtained from a rock quarry situated on the southern side of Neer's Hill, two miles north of Santa Rosa. The locality is less than a half mile east of the state highway and 200 yards northeast of the dirt road which runs eastward from the highway. Neer's Hill lies in the south-central portion of Section 11, Range 8 west, Township 7 north.

The exposure is about 50 feet high and consists of two layers of massive, tufaceous sandstones separated by a thinner layer of extremely fine, pure, volcanic ash containing the leaf impressions. The structure in the cut seems to be that of a small anticlinal fold, with its steepest dip about 35° toward the east, probably a result of movement along the line of the Hayward fault, whose surficial expression is shown in the abrupt rise of the hills out of the level Santa Rosa Valley, less than a half mile west of the locality.

The intercalation of sandstones and tuffs has already been noted in this vicinity by Dickerson,¹ who refers the sandstones to the Merced and the tuffs to the Sonoma group. Such interfingering of sandstones containing marine invertebrates and volcanic ash containing terrestrial plants is significant of the strand-line conditions under which they were deposited and extremely helpful in the correlation of plant materials from other localities where the stratigraphic and paleontologic relations are not so apparent. The position of the leaf impressions, flat-lying along the bedding planes, and the purity and fineness of the ash suggest rapid accumulation in the quiet water of a shallow marine embayment in which the tufaceous sandstones were accumulating, affected in their lithological continuity only by periodic showers of fine ash which was deposited more quickly, enclosing the leaves and other plant materials derived from the nearby shores.

Most of the leaves at this locality were collected from the heap of rock fragments lying at the base of the cut, as it was impossible to ascend the steep escarpment to the outcrop of the ash. No leaf impressions were discovered in the sandstones, which make up the greater part of the exposure, the ash layer being only about 3 feet thick. Ten species are recorded from this locality arranged here as in the above lists, according to their order of dominance:

<i>Quercus declinata</i>	<i>Castanopsis chrysophylloides</i>
<i>Platanus paucidentata</i>	<i>Salix coalingensis</i>
<i>Quercus orindensis</i>	<i>Sequoia langsdorffii</i>
<i>Pseudotsuga sonomensis</i>	<i>Fraxinus caudata</i>
<i>Populus alexanderi</i>	<i>Ilex sonomensis</i>

WILDCAT FORMATION

Two fossil leaf localities were discovered during the summer of 1928 in the upper portion of the Wildcat formation² of Humboldt

¹ Dickerson, Cal. Acad. Sci., 4th ser., vol. 11, No. 19, 544. 1922.

County. This formation is exposed to a thickness of several thousand feet along the south fork, as well as the main fork, of the Eel River, whose flood plain truncates its upper beds near Garberville. Its structure is that of a gently folded syncline whose strike follows the general course of the Eel River from northwest to southeast. The entire formation rests unconformably on the highly folded and faulted Mesozoics, including the Knoxville, Horsetown and Chico formations of the Cretaceous and the Franciscan formation of the Jurassic.¹

On the basis of invertebrate material collected from the Wildcat formation, B. L. Clark correlates it with the Merced formation of central California and the Etchegoin of the San Joaquin Valley.² Both of these formations are referred to the lower to middle Pliocene.³

The typical wildcat fauna, as listed by Clark in a letter to Dr. J. C. Merriam,⁴ includes the following species, of which those starred are especially critical stratigraphically:

<i>Alectron</i> cf. <i>moriana</i> Martin	<i>Siliqua lucida</i> Conrad
<i>Anomia</i> sp.	<i>Solen</i> sp.
* <i>Paphia staleyii</i> Gabb.	<i>Spisula albaria</i> Conrad
<i>Pecten</i> sp.	* <i>Spisula voyii</i> Gabb.
<i>Pecten</i> sp.?	<i>Spisula</i> sp.?
* <i>Schizothærus pajaroensis</i> Conrad	<i>Tellina aragonita</i> Dall

LOCALITY 155

A collection of leaves was obtained from an outcrop a quarter of a mile up the creek which flows into the south fork of the Eel River, a mile and a half north of Garberville. The creek runs under the Redwood Highway at the end of a steep escarpment flanking the eastern side of the road.

The section consists of 500+ feet of alternating yellow to buff sandstones and conglomerates. Carbonized wood occurs scattered throughout; leaves occur in a buff sandstone a quarter of a mile upstream from and approximately 125 feet in vertical distance above the floor of the creek below the Redwood Highway bridge. One distinct layer of leaves occurs along a bedding plane; others are scattered in the overlying 3 to 4 feet of sandstone. Strike of the beds: north 60° west; dip: 20° northward. The following species have been recognized:

<i>Salix coalingsensis</i>	<i>Fraxinus caudata</i>	<i>Platanus paucidentata</i>
<i>Alnus merriami</i>	<i>Populus alexanderi</i>	<i>Umbellularia oregonensis</i>

LOCALITY 156

A second horizon was discovered one mile up the creek, locally known as Bear Canyon Creek, which flows under the first concrete bridge north of Garberville. This bridge is approximately a quarter of a mile north of town on the Redwood Highway.

¹Dept. Int. Press Mem. and accompanying map by Hoots, Mar. 5, 1928.

²Clark, Oral communication, Sept. 12, 1929.

³Clark, *Stratigraphy and Faunal Horizons of the Coast Ranges of California*, frontispiece, correlation table, 1929.

⁴Chaney, Written communication, May 5, 1930.



FIG. 1—Valley of south fork of Eel River, one mile north of Garberville, Humboldt County, California, near Localities 155 and 156. Wilcat formation is shown exposed along east side of Redwood Highway, which runs along eastern side of river in this vicinity.

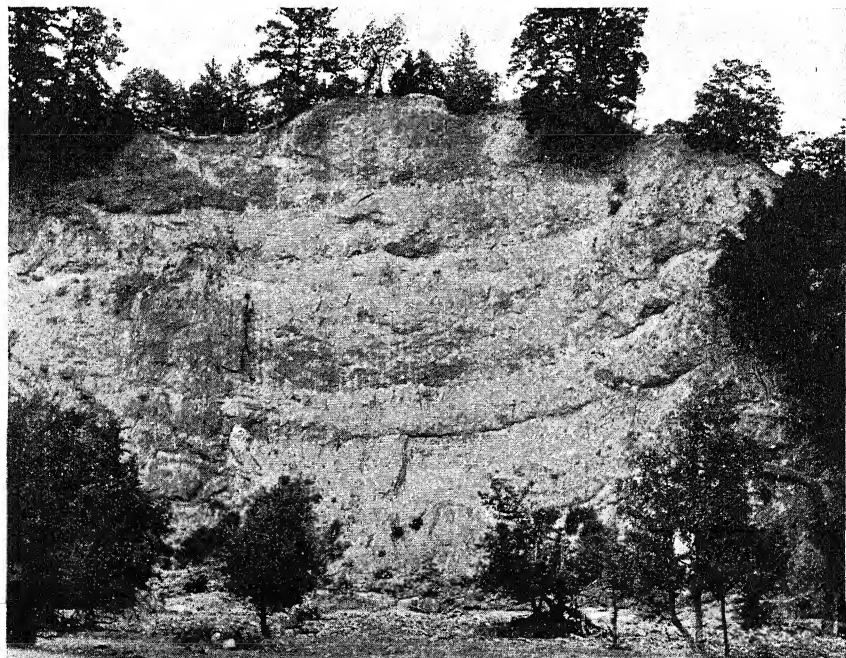


FIG. 2—An exposure of sandstones and conglomerates of Wilcat formation at Locality 157, on north side of east branch of Eel River, about 4

The section consists of 1000+ feet of buff to gray, massive sandstones and coarse conglomerates. Carbonized wood is scattered throughout; leaves occur in a gray, shaly sandstone in the north fork of the creek, 600 feet above the main fork, approximately one mile in walking distance and 100 feet in vertical distance above the junction of the creek and the south fork of the Eel River. The best horizon is in the south wall of the creek just above its floor. Leaves generally occur as carbonaceous impressions. Strike and dip of the beds are the same as in above locality.

Although over 150 leaf specimens were collected at this locality, only five species have been encountered. These are listed below in order of their numerical dominance:

Fraxinus caudata

Populus alexanderi

Alnus merriami

Salix coalingsensis

Platanus paucidentata

LOCALITY 157

Two additional genera, *Sequoia* and *Pseudotsuga*, are represented by petrified wood collected from the Wildcat formation by Dr. R. W. Chaney and determined by Mrs. Irma E. Webber. This material was encountered in beds of the same lithological and structural characters as those studied by the writer, and less than 3 miles distant from the above localities. Most of it was collected in an exposure of yellow to gray sandstones and conglomerates 3.5 miles up the eastern tributary of the south fork of the Eel River from the Hotel Benbow, which is situated on the Redwood Highway 2.5 miles south of Garberville. Mrs. Webber's determinations on the wood indicate a very close relationship, if not identity, with the modern species, *Sequoia sempervirens* and *Pseudotsuga taxifolia*.

MERCED FORMATION

Two fossil plant localities have been found in the Merced sandstone of the San Francisco Bay region. The Merced formation is one of the thickest and most widespread marine deposits in California and has been extensively studied, both stratigraphically and paleontologically. The formation was named by Lawson¹ from a study of the admirable exposure along Seven Mile Beach, a few miles south of the Golden Gate. The beds are here seen to constitute a 5800 foot thickness of marine clays, sandy shales, sandstones, fine pebbly conglomerates and shell beds. The lower portion, exposed from Mussel Rock north to Thornton Station, strikes north 40° to 60° west, and dips 50° to 60° northeastward; the upper portion, north of Thornton Station, dips considerably less, approaching horizontality.² The formation rests unconformably on Franciscan

¹Lawson, Univ. Calif. Dept. Geol. Bull., vol. 1, No. 4, 143, 1893.

²Martin, Univ. Calif. Dept. Geol. Bull., vol. 9, No. 15, 224, 1916.

volcanics. On the basis of large collections of invertebrates the beds have been referred to the middle Pliocene, though recent investigations indicate that their basal portions are probably equivalent to the Jacalitos¹ of lower Pliocene age, and their upper portions may extend well into the upper Pliocene, or possibly even into the Quaternary.²

One of the largest occurrences of the Merced sandstone outside of the type locality, described above, is in the Santa Rosa valley, near the town of Santa Rosa, where the sandstones are closely associated and intercalated with the volcanics of the Sonoma group, as has already been mentioned in the descriptions of the Sonoma tuff localities.

Aside from its stratigraphical equivalence to the Sonoma group, the Merced is thought to be correlated as well with the Wildcat formation of Humboldt County and the Etchegoin of the San Joaquin Valley.³ This is particularly significant in the present study since plant remains have been collected from each of these formations.

Plant material is by no means abundant in the Merced sandstones, due, no doubt, to their marine character. Lawson⁴ has reported the occurrence of cones of *Pinus insignis* in a portion of the beds which has since been referred to the Quaternary.⁵ The same author⁶ also has reported *Pseudotsuga* cones from the lower Merced north of Mussel Rock, where Mason has recently discovered the same as well as another type of cone. No plant remains have hitherto been reported from the Merced exposures near Santa Rosa.

LOCALITY 158

Leaf impressions have been discovered in an exposure of buff-colored, tufaceous sandstone a half mile southeast of Lakeville in a cut on the dirt road which runs eastward a quarter mile south of that town. This road intersects the Lakeville road one mile south of the main highway connecting Petaluma and Sonoma. The hill to the south of the cut is capped with white tuffs. The underlying Franciscan rocks were observed in an old quarry a half mile eastward, just north of the road.

It is apparent that here again we are concerned with an alternation of sandstones and tuffs, belonging to the Merced and Sonoma groups respectively such as was encountered north of Santa Rosa. Although fossil invertebrate evidence is lacking, the intimate association of the sandstones and tuffs at this locality and the lithology

¹ Clark, Oral communication, Sept. 12, 1929.

² Martin, op. cit., 228.

³ Clark, Oral communication, Sept. 12, 1929.

⁴ Lawson, San Francisco Folio, 14, 1914.

⁵ Ashley, Proc. Cal. Acad. Sci., 2d ser., vol., 5, 312, 1896.

⁶ Lawson, op. cit., 14.

of the sediments make its reference to the Merced, previously made by Dickerson,¹ rather unquestionable. The evidence of the fossil plants clearly verifies this reference. Seven species, arranged here in order of dominance, have been collected at this locality:

<i>Platanus paucidentata</i>	<i>Castanopsis chrysophylloides</i>
<i>Quercus lakevillensis</i>	<i>Salix coalingensis</i>
<i>Umbellularia oregonensis</i>	<i>Alnus merriami</i>
<i>Populus fremontii</i>	

LOCALITY 159

A small collection of carbonized cone material has recently been made from the type exposure of the Merced sandstones by H. L. Mason of the University of California. The cones were partially exposed in the sea-cliffs 2 miles north of Mussel Rock in the steeply dipping sandstones of the Lower Merced, in the vicinity of the location from which cone material had previously been discovered by Lawson (see page 16). Only two species occur here: *Pseudotsuga sonomensis* and *Pinus masoni*.

SANTA CLARA FORMATION

The Santa Clara beds were first described by Lawson,² who regarded them as delta deposits in the interior valley whose northern extension coincides with the southern arm of San Francisco Bay. Their deposition was contemporaneous with the upper portion of the Merced sandstones of middle Pliocene age, which occupied the northern end of the same valley. In the following year Cooper,³ on the basis of invertebrates, described the beds as fresh-water gravels and alluvium of Pliocene age. Arnold⁴ was of the same opinion. In the Santa Cruz Folio, by Branner, Newsome and Arnold, the beds are described as contemporaneous with a portion of the Merced sandstones, and as being made up of gravels, sands and clays laid down in great fresh-water lakes to a thickness of at least 500 feet. Paleontologically they were referred to the upper Pliocene or lower Quaternary. Clark's recent correlation table⁵ makes them equivalent to the Paso Robles formation, so well developed in the Santa Lucia Mountains.

As Hannibal has already pointed out,⁶ it is not likely that the Santa Clara beds could have been deposited at any great elevation. A study of the geological history of the entire bay region seems to indicate that during upper Pliocene time this section of California was subjected to an uplift of rather limited proportions. Even if

¹ Dickerson, Proc. Cal. Acad. Sci., 4th ser., vol. 11, 548, 1922.

² Lawson, Univ. Calif. Dept. Geol. Bull., vol. 1, No. 4, 152, 1893.

³ Cooper, Proc. Cal. Acad. Sci., 2d ser., vol. 4, 171, 1894.

⁴ Arnold, Proc. U. S. Nat. Mus., vol. 34, 355, 1908.

⁵ Clark, *Stratigraphy and Faunal Horizons of the Coast Ranges of California*, frontispiece, 1929.

⁶ Hannibal, Bull. Torrey Bot. Club., vol. 38, 330, 1911.

considerable uplift had taken place it is doubtful whether any large lakes could have maintained themselves, particularly in so open a valley as the Santa Clara, in which there is no evidence of a transverse barrier to have blocked its easy drainage toward the bay.

LOCALITY 160

Fossil plants from the Santa Clara lake beds have previously been described by Hannibal¹ from five localities in the Santa Cruz Mountains. Only one of these has yielded any considerable number of specimens in the writer's collections, namely, the Calabazas Canyon locality, situated 1.75 miles north 10° west of Saratoga. The beds are exposed in the floor and walls of the creek near the second bridge on a gravel road, a mile west of the paved highway to Sunnyvale. This gravel road joins the highway just south of Miller's service station, 1.5 miles north of Saratoga.

The observed section consists of alternating beds of massive, fine, buff-colored conglomerates; sandy to shaly, blue or buff-colored sandstones; and thin layers of bluish shale; the series strikes north 25° west and dips 50° northeast, and is overlain unconformably by horizontal gravels of valley alluvium. The rocks, particularly the shales and shaly sandstones, are considerably shattered and slickensided by local movements.

Most of the leaves occur in the shaly portions of the buff sandstone, though occasionally in the bluish shales. The majority are carbonaceous, some, in fact, preserving the actual leaf in a thin, fragile, carbonaceous film. The following species, arranged in their order of dominance, have been collected at this locality:

<i>Quercus hannibali</i>	<i>Populus alexanderi</i>
<i>Salix coalingensis</i>	<i>Alnus merriami</i>
<i>Ribes stanfordianum</i>	<i>Libocedrus</i> sp.
<i>Salix</i> sp.	<i>Pinus</i> sp.
<i>Pteris calabazensis</i>	<i>Pseudotsuga sonomensis</i>
<i>Ceanothus chaneyi</i>	<i>Cercocarpus cuneatus</i>
<i>Amelanchier</i> sp.	<i>Prunus merriami</i>

Many of the above species were also observed in Hannibal's collections at Stanford University, which were obtained at the same or nearby localities in the Santa Clara beds. Hannibal regarded his specimens as leaves of living species, which is, in the writer's opinion, perfectly possible but uncorroborated because of the failure of the sediments to preserve those diagnostic portions of the plants which are necessary to establish specific identity. A tentative revision of Hannibal's species has already been made by Chaney.²

Three species, which have not been encountered by the writer, are represented by specimens in the Stanford University collections.

¹ Hannibal, Bull. Torrey Bot. Club, vol. 38, 329, 1911.

² Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 45, 1925.

None of the species is common in the collections nor represented by more than a few fragmentary specimens.

The first of these, *Sequoia langsдорffii*, is the fossil equivalent of the modern redwood, *S. sempervirens*, to which species Hannibal¹ had previously referred the specimens. The second, *Æsculus* sp., is the writer's reference of several specimens which Hannibal had referred to *Rhamnus purshiana*.² The third, *Arbutus* sp., is the provisional reference of the specimens which had been identified with the modern *Arbutus menziesii*.³ The species are reported as "not common" or "rare"⁴ at the Portola locality and entirely absent at Calabazas Canyon.

PICO FORMATION

A small collection of cone material has been collected from the Pico formation near Ventura. This formation is confined to southern California, being particularly well exposed north and east of Ventura. The Pico and the Saugus, or the marine equivalent of the latter, the Los Posas formation,⁵ constitute the lower and upper portions of the Fernando group,⁶ which is typically underlain by the Modelo⁷ or Santa Margarita⁸ formation of upper Miocene age and overlain by Pleistocene terrace deposits. Marine sandstones, clays, and conglomerates to a thickness of about 13,000 feet make up the Pico formation. The entire thickness has been variously folded and faulted since its deposition. On the basis of invertebrates, which are common throughout the section, Clark⁹ correlates the basal portion of the Pico with the Jacalitos, the middle portion with the Etchegoin, and the upper portion with the Santa Barbara, San Pedro and San Diego Pliocene. Cartwright¹⁰ has recently divided the Pico into a lower and an upper division, mainly on lithological evidence.

LOCALITY 161

The writer's attention was directed to the occurrence of carbonized cones in the Pico by Mr. Harold K. Pieper of the Associated Oil Company, at Ventura. The locality is situated on the tidal flats along the coast highway 6 miles northwest of Ventura, in a half-mile exposure of finely laminated dark gray or blue-gray clays and sands. According to Cartwright's geological map of the region¹¹

¹ Hannibal, Bull. Torrey Bot. Club, vol. 38, 336, pl. 15, fig. 3, 1911.

² Hannibal, op. cit., 338, pl. 15, fig. 10.

³ Hannibal, op. cit., 339, pl. 15 fig. 1.

⁴ Hannibal, op. cit., 335.

⁵ Clark, *Stratigraphy and Faunal Horizons of the Coast Ranges of California*, 27, 1929.

⁶ Kew, U. S. Geol. Surv. Bull. 753, 69, 1924.

⁷ Kew, op. cit., 70.

⁸ Waterfall, Univ. Calif. Dept. Geol. Bull., vol. 18, No. 3, 75, 1929.

⁹ Clark, op. cit., 26.

¹⁰ Cartwright, Amer. Assoc. Pet. Geol., Bull. 12, No. 3, 237, 1928.

¹¹ Cartwright, op. cit., 247, 1928.

the beds are situated in the southern limb of a sharply folded anticline in the lower Pico, which has been truncated by marine wave action.

The plant material includes carbonized cones, wood and individual cone scales, occurring in lignitic seams 0.5 to 2 inches thick. Most of the material, with the exception of a few rather complete cones, is fragmentary and macerated, suggesting wave action on a deltaic deposit in a shallow marine embayment. Only two species have here been recognized: *Pinus pieperi* and *Pinus masoni*.

ORINDA FORMATION

Two plant localities have been discovered in the Orinda formation of the Berkeley Hills east of San Francisco Bay. The Orinda formation consists of an accumulation of about 5000 feet¹ of fresh-water and alluvial clays, shales, sandstones, conglomerates and tuffs, with occasional beds of limestone. The beds lie conformably on the Pinole tuff or, where the tuff is missing, rest unconformably on the Miocene San Pablo or Monterey, or in places directly on the older Franciscan series.² They are overlain by the Berkeley group consisting of the Moraga andesites and basalts, the Siesta sandstones and shales, and the Bald Peak basalts.³ The structure of the Orinda formation is that of a synclinal trough with subordinate folds.

No marine fossils have been discovered in the formation, but fresh-water invertebrates, particularly ostracods, are recorded, and considerable vertebrate material has been found.⁴ On the basis of both the invertebrates and the vertebrates the formation has been referred to the Pliocene. From its stratigraphic relations to the Pinole tuff, which is petrographically similar to the Sonoma tuff, Lawson has expressed the view⁵ that "the Orinda is the fresh-water equivalent of the Merced, laid down in an interior diastrophic trough and shut off from the sea by a ridge corresponding in position and trend with the present Berkeley Hills." Clark has recently⁶ correlated the formation with the Jacalitos of the San Joaquin Valley, which he considers the equivalent of the lower Merced of central California.

LOCALITY 163

Considerable leaf impressions were recently discovered by V. L. Vanderhoof of the University of California in the Orinda beds near the Lafayette Dam. The locality, which was visited by the writer

¹ Penck, Science, n. s., vol. 69, 194, 1929.

² Lawson, U. S. Geol. Surv., San Francisco Folio, 13, 1914.

³ Clark, *Stratigraphy and Faunal Horizons of the Coast Ranges of California*, frontispiece table, 1929.

⁴ Merriam, Univ. Calif. Dept. Geol. Bull., vol. 7, No. 19, 373, 1913.

⁵ Lawson, op cit., 13.

⁶ Clark, Oral communication, Sept. 12, 1929.

and H. L. Mason during the summer of 1929, is situated 500 feet southwest of the Lafayette Dam, in the upper shelf of the excavations. The dam lies 1.25 miles west 30° south of the town of Lafayette, which is situated at the head of Pleasant Valley in the Berkeley Hills of Contra Costa County. The exposure consists of northwestwardly dipping gravels and fine to coarse sandstones. The gravels are considerably cross-bedded and irregular, suggesting river deposition. The entire escarpment shows evidence of faulting and shattering.

The plant material occurs in the layers of finer sandstone, along the bedding. While the preservation is far from perfect, a considerable collection was obtained, in which the following species, in order of dominance in the collections, have been recognized:

<i>Platanus paucidentata</i>	<i>Fraxinus caudata</i>
<i>Salix</i> sp.	<i>Rhus</i> sp.
<i>Salix coalingensis</i>	<i>Prunus merriami</i>
<i>Populus alexanderi</i>	<i>Populus prefremontii</i>
<i>Ulmus brownellii</i>	<i>Quercus orindensis</i>

LOCALITY 162

A second collection of leaves from the Orinda formation was obtained from a road cut 0.75 of a mile approximately north of St. Mary's College, which is situated one mile northwest of the town of Moraga, Contra Costa County. The leaves were discovered by H. L. Mason during the summer of 1928 in a recent excavation along the new road which runs north and south along the eastern side of Las Trampas Creek. Most of the material was obtained at the northeast corner of the junction between the new road and the old road, which runs southeastward along Las Trampas Creek, past the college reservoir and dam. The exposures along the new road consist of about 1600 feet of buff sandstones and conglomerates, and bluish-gray shales, striking in a general northwest-southeast direction, and dipping 45° toward the southwest. The same series of beds, containing scattered plant fragments, may be observed less than 0.25 mile west of the locality, in the cuts along the Oakland, Antioch and Eastern Railway tracks. The beds are overlain unconformably by horizontal beds of sandy and conglomeratic alluvium.

The better leaf impressions occur in the indurated, fine sandstone and are mainly scattered throughout the horizons, rather than confined to the bedding planes. Several specimens were collected from the fragments at the base of the cut. The following species, arranged in order of their abundance in the collections, have been recognized:

<i>Quercus hannibali</i>	<i>Salix</i> sp.	<i>Prunus merriami</i>
<i>Quercus orindensis</i>	<i>Populus alexanderi</i>	<i>Salix coalingensis</i>
<i>Rhus</i> sp.	<i>Platanus paucidentata</i>	<i>Populus prefremontii</i>

ETCHEGOIN FORMATION

A small collection of well-preserved leaf impressions was recently secured from the Etchegoin beds southeast of Coalinga. The Etchegoin formation, typically exposed in the San Joaquin valley north and south of Coalinga, consists of an alternating series of but slightly indurated sands, gravels, and clays, to a thickness of about 3500 feet. Both paleontologically and lithologically they seem to represent conditions transitional between the marine Jacalitos formation, lying conformably below them, and the continental Tulare formation above. Throughout the entire Etchegoin period of deposition there is evidence of an alternation of marine and brackish, or even fresh-water conditions, producing the lenticular masses of conglomerates and coarse clastics interspersed with even more continental facies containing both plant and vertebrate remains, coal and gypsum.¹

Originally referred to the upper Miocene by Arnold,² the Etchegoin has more recently been definitely placed in the Pliocene on the basis of both invertebrate³ and vertebrate⁴ collections. Compared with the marine Pliocene of central and northern California, Clark⁵ considers it the correlative of the Merced or the Wildcat.

LOCALITY 164

The Etchegoin plant locality was discovered by Mr. Alfred Livingston of the University of California. It is situated 8 miles south 36° east of Coalinga, in the south-central portion of Section 30, Township 21 south, Range 16 east. The section observed on the slopes of a northwardly directed ravine consists of interbedded fine and coarse sands, mostly unindurated, to fine-grained tufaceous sandstones and sandy shales, striking north 50° west and dipping 10° to 12° northeastward. Lenses of fine conglomerates and indurated limonitic sandstones are intercalated throughout the series. The principal collections come from a ledge of lenticular, limonitic sandstone on the northern slope and 75 feet down from the top of a bare ridge which runs in a northeasterly direction toward an old deserted ranch-house. The leaves occur in both the limonitic layer and the light-colored sandstone just below it. Leaves of the same species occur also in a thin shale horizon on the upper slopes of the hill just west of the ranch-house. This horizon is stratigraphically about 90 feet above the first location, and 4 feet below a reddish, limonitic sandstone which contains an abundance of marine invertebrates,

¹ Nomland, Univ. Calif. Dept. Geol. Bull., vol. 10, No. 14, 204, 1917.

² Arnold, U. S. Geol. Surv. Bull. 396, 28, 1909.

³ Nomland, op. cit., 225-228.

⁴ Merriam, Univ. Calif. Dept. Geol. Bull., vol. 9, No. 4, 56, 1915.

⁵ Clark, Oral Communication, Sept. 12, 1929.

particularly echinoids, corals and pectens. A small collection of these was submitted to Dr. B. L. Clark, who identified them as follows: *Pecten coalingensis* Arnold, *Dendraster arnoldi* Twitchell, *Astrangia coalingensis* Vaughan.

Clark also informed the writer that this is Arnold's type locality for the *Pecten coalingensis* zone of the upper Etchegoin.

Although an abundance of plant material was collected at these horizons, the number of species encountered is surprisingly low, being limited to the following, again arranged in their order of dominance:

Salix coalingensis
Platanus paucidentata
Fraxinus caudata

Garrya masoni
Populus alexanderi
Quercus orindensis

ALTURAS FORMATION

A small flora has been collected by Miss Annie M. Alexander and Miss Louise Kellogg from a point near Alturas, Modoc County. The beds, which are here referred to as the Alturas formation, consist of gray, sandy tuffs and shales, containing both plant and vertebrate remains. The mammalian remains collected by Stock appear to indicate an upper Pliocene age for the beds.¹

LOCALITY 165

The tuffs containing the well-preserved leaf impressions are exposed on Rattlesnake Butte, about 4 miles east of Alturas. Although over 25 specimens have been examined, only two species have been encountered in the collection: *Populus alexanderi* and *Salix coalingensis*.

COMPOSITION OF THE FLORA

QUALITATIVE CONSIDERATIONS

The Pliocene floras of California comprise 36 species, representing 28 genera and 22 families. The species are unevenly distributed among four groups and include 2 ferns, 6 conifers, 1 monocotyledon, and 27 dicotyledons.

All of the dicotyledonous species are represented by leaf impressions; 3 of the conifers are represented by cone material, 2 by cone material and leaf impressions, and one by leaf impressions only. Dicotyledonous fruits are rare, only one species, *Quercus hannibali*, being represented by a few, rather poorly preserved acorn cup impressions.

Petrified wood is common at most of the localities. Although this has not yet been comprehensively studied, a number of wood determinations have been made by Mrs. Irma E. Webber and Charles Read, of the University of California. Pliocene petrified wood has

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 32, 45, 1925.

previously been reported and studied by M. C. White¹ of New Haven and P. Platen² of Germany. All of the genera based on wood structure are represented by corresponding genera based on leaves.

The Pliocene floras may be conveniently divided into six groups, based on the associations of closely related living species: (1) The Redwood element, including those species whose living equivalents are dominant in the coast redwood forest of California; (2) the Sierra-Cascade element, including the species whose living equivalents are dominant in the montane forest of the Sierra Nevada, Cascades, and higher Coast Ranges; (3) the Broad-sclerophyll element, including the species whose living equivalents are dominant in the broad-sclerophyll forests³ of the lower Coast Ranges and Sierra foothills; (4) the Chaparral element, including the species whose living equivalents are dominant in the climax chaparral of the more xerophytic portions of the lower Coast Ranges and Sierra foothills; (5) the Riparian⁴ element, including the species whose living equivalents are dominant in the lowland stream-bank formations of the southern Coast Ranges and intermontane valleys; (6) the Exotic element, including the species whose living equivalents are not found associated with the present vegetation of California. This grouping is represented in the following tabular form.

TABLE 2

	Number of species	Percentage of total species	Percentage of total occurrences
Redwood element.....	6	16.7	15.5
Sierra-Cascade element.....	4	11.1	4.1
Broad-sclerophyll element.....	7	19.4	15.5
Chaparral element.....	9	25.0	16.5
Riparian element.....	7	19.4	44.3
Exotic element.....	3	8.4	4.1
Totals	36	100.0	100.0

The second column in table 2 represents merely the proportion of the various elements to the total number of recorded species, regardless of their distribution among the various localities. This tends to overestimate those species which occur at only one or two localities and underestimate those which are found in a number of localities. For this reason the third column has been added, showing the proportion of the elements to their total representation, according to the number of occurrences of their component species at all the Pliocene localities, shown in the accompanying distribution table 3.

¹ Marsh, Amer. Jour. Sci. and Arts, 3d ser., vol. 1, 268, 1907.

² Platen, Natur-Forsch. Gesellsch. zu Leipzig, 4-26, 1907.

³ For complete discussion of the Broad-sclerophyll Forest and Climax Chaparral of California see Cooper, Carnegie Inst. Wash. Pub. No. 319, 1922.

⁴ This term is used throughout the report to include only the riparian element of the more xerophytic portions of the southern Coast Ranges and interior valleys.

TABLE 3

	Sonoma						Wildcat			Merced		Santa Clara	Pico	Orinda		Etohe- goin	Alturas
	Petrified Forest		Bennett Valley	Santa Rosa	Garberville			Lakeville	Mus-sel Rock	Calabazas Canyon	Ventura	St. Mary's College	Lafayette Dam	Coal-inga	Alturas		
	150	151	152	153	154	155	156	157	158	159	160	161	162	163		164	165
Locality																	
Redwood Element:																	
Sequoia langsdorffii.....	×	×	×	×	×		×	×				×					
Pseudotsuga sonomensis.....	×																
Pinus masoni.....																	
Woodwardia bennettii.....				×													
Odotemon hollicki.....	×																
Smilax sp.....	×																
Broad-sclerophyll Element:																	
Castanopsis chrysophylloides.....			×		×												
Quercus lakevillensis.....	×	×		×													
Quercus harrimbali.....													×				
Quercus declinata.....			×		×												
Umbellularia oregonensis.....	×	×				×											
Aesculus sp.*.....																	
Arbutus sp.*.....																	
Chaparral Element:																	
Heteromeles sp.....	×																
Cercocarpus cuneatus.....																	
Rhus sp.....																	
Prunus merriami.....																	
Garrya masoni.....			×														
Pinus pieperi.....																×	
Amelanchier sp.....																	
Ceanothus chaneysii.....																	
Quercus orindensis.....					×											×	
Riparian Element:																	
Populus alexanderi.....			×		×		×	×								×	×
Salix coalingsensis.....					×		×	×								×	×
Platanus paucidentata.....			×		×		×	×								×	
Alnus merriami.....			×		×		×	×									
Fraxinus caudata.....					×		×	×									
Populus fremontii.....																	
Salix sp.....			×														
Sierra-Cascade Element:																	
Pinus sp.....																	
Libocedrus sp.....																	
Ribes stanfordianum.....																	
Pteris calabazensis.....																	
Exotic Element:																	
Ilex sonomensis.....	×					×											
Ulmus brownellii.....																	
Quercus bockeei.....	×																
											</						

THE REDWOOD ELEMENT

The mere presence of *Sequoia* and its associates in the Pliocene flora at once suggests conditions not unlike those existing in portions of California at the present time. The modern *Sequoia sempervirens* Endl. is the dominant species of the Redwood or Coast Range forest of the northern and central Coast Ranges of the Pacific Coast. This forest lies chiefly in the Transition life zone, from sea-level to 2000 or 3000 feet and is entirely coastal in its distribution. It is best developed in the humid Coast Ranges of northwestern California, becomes scattered and mixed with the more mesophytic of the broad-sclerophyll elements in the central Coast Ranges, and is confined to but a few areas in the southern Coast Ranges, where conditions of humidity are only locally favorable, producing patches of redwoods and their hardier associates, surrounded by the more xerophytic of the broad-sclerophyll elements and by chaparral species and, along the stream-banks, by the characteristic riparian species.

The following list shows the fossil species of the Redwood element and their nearest relatives.

Fossil species:

Sequoia langsdorffii (Br.) Heer
Pseudotsuga sonomensis Dorf
Pinus masoni Dorf
Woodwardia bennetti Dorf
Odostemon hollicki Dorf
Smilax sp.

Living species:

Sequoia sempervirens Endl.
Pseudotsuga taxifolia Brit.
Pinus muricata D. Don.
Woodwardia radicans Sm.
Odostemon aquifolium Pursh.
Smilax californica (A. DC.) A. Gray.

This compilation by no means implies that the species listed are found only in the redwood forest. It is obvious that in any artificial grouping of elements according to associations it is difficult to indicate the overlapping of species which takes place in the transition from one association to another, and to relegate species of widespread distribution to their most characteristic association. *Pseudotsuga taxifolia*, for example, is also common in both the Sierra-Cascade forest and the broad-sclerophyll forest, and is even present along streams in areas dominated by chaparral. Similarly, *Woodwardia radicans* and *Odostemon aquifolium* are by no means confined to the redwood forest, being common in local mesophytic situations of both the broad-sclerophyll forest and the chaparral. As a basis for the more detailed discussion of the individual Pliocene floras, the species are merely tentatively grouped with the association in which they seem to be dominant.

It is significant that neither the above list nor the following lists include many of the most characteristic redwood associates, including such species as *Myrica californica* Cham., *Acer macrophyllum* Pursh., *Corylus rostrata* Ait. var. *californica* A. DC., *Rhamnus purshiana* DC., and *Cornus nuttallii* Aud., species which are admirably situated

in the redwood forest for preservation in the basins of deposition. The absence of Pliocene relatives of such species suggests conditions unfavorable for the growth of an extensive redwood forest, a suggestion which is amply corroborated by the limited distribution of the few redwood elements in the Pliocene record and by their scarcity at the individual localities. The abundance of broad sclerophyll, chaparral and riparian species in the floras is likewise indicative of only a scattered growth of the redwood elements during the Pliocene. A complete discussion of the various associations and their significance and relation to the redwood forest will be given on a later page.

THE SIERRA-CASCADE ELEMENT

There are several species present in the Pliocene floras which indicate a relationship to species of the modern Sierra-Cascade forest, which dominates the Transition life zone of the Sierra Nevada and Cascade Mountains and overlaps into both the northern and southern Coast Ranges. It is generally found at the middle altitudes, from 2500 to 6000 feet above sea-level, though it occurs at somewhat lower levels toward the north and higher levels toward the south of its range. It is dominated by coniferous elements, including *Pinus lambertiana* Dougl., *P. ponderosa* Dougl., *P. jeffreyi* Murr., *Libocedrus decurrens* Torr., *Abies concolor* Lindl., and *Pseudotsuga taxifolia* Brit. The broad-leaved associates of the Sierra-Cascade forest include many chaparral species, a few broad-sclerophyll species and a number of riparian species along the stream valleys.

The following species, listed with their nearest living relatives, are the members of this group,

Fossil species:

Pinus sp.
Libocedrus sp.
Ribes stanfordianum Dorf
Pteris calabazensis Dorf

Living species:

Pinus lambertiana Dougl.
Libocedrus decurrens Torr.
Ribes nevadense Kell.
Pteris aquilina L. var. *lanuginosa* (Bory).

This list would be considerably augmented by the addition of those species which are commonly associated with the above-mentioned living species but are dominant in another forest or association. *Pseudotsuga taxifolia* might, indeed, be considered of greater importance in the Sierra-Cascade forest than in the redwood forest. Many of the chaparral species, notably *Ceanothus integerrimus* H. & A., *Amelanchier alnifolia* Nutt., *Cercocarpus betuloides* Nutt., and *Garrya fremontii* Torr., are common undershrubs in the Sierra-Cascade forest, and *Pinus sabiniana* Dougl. is present along its lower borders. The stream borders within the forest are frequently lined with typical riparian species, including willows, poplars and alders.

None of the fossil species of the Sierra-Cascade element is widely distributed in the Pliocene record. Those listed above are recorded

from only one locality, where they are associated with chaparral species of Sierran aspect and a few riparian species. The discussion of this flora, the Santa Clara, is given in detail on a later page.

THE BROAD-SCLEROPHYLL ELEMENT

Several Pliocene species are closely related to living species of the broad-sclerophyll forest, which ranges through the upper Sonoran and lower Transition life zones of the Coast Ranges and Sierra Nevada foothills. This forest never dominates the country as the conifer forests do, occurring rather as discontinuous patches alternating with patches of chaparral. It is most important in the central Coast Ranges, becoming transitional to the redwood forest toward the north and giving way to the chaparral toward the south. Vertically, it overlaps upward into the conifer forests and downward into the chaparral. Both laterally and vertically it represents the degree of mesophytism between the chaparral and the conifer forests of the Coast Ranges and Sierra Nevada. The forest is dominated particularly by the live-oaks, including *Quercus agrifolia* Née, *Q. chrysolepis* Liebm., and *Q. engelmanni* Greene; and by *Castanopsis chrysophylla* A. DC., *Umbellularia californica* Nutt., *Arbutus menziesii* Pursh., *Pasania densiflora* Oerst., *Acer macrophyllum* Pursh., and *Æsculus californica* Nutt. Several of these are represented by fossil equivalents in the Pliocene:

Fossil species:

Castanopsis chrysophylloides Lesq.
Quercus lakevillensis Dorf
Quercus hannibali Dorf
Quercus declinata Dorf
Umbellularia oregonensis Chauey
Æsculus sp.
Arbutus sp.

Living species:

Castanopsis chrysophylla A. DC.
Quercus agrifolia Née
Quercus chrysolepis Liebm.
Quercus tomentella Engelm.
Umbellularia californica Nutt.
Æsculus californica Nutt.
Arbutus menziesii Pursh.

The inclusion of *Quercus tomentella*, which is confined to the islands off the southern California coast, might be questioned. On both Santa Rosa and Santa Cruz Islands it is found associated with live oaks and a few chaparral and riparian species, suggesting a relationship to the broad-sclerophyll element of the mainland. Two of the living species mentioned above are important constituents of other forests as well: *Umbellularia californica* is a frequent associate of *Sequoia sempervirens* in the redwood forest, and *Quercus chrysolepis* is an important species in the chaparral; both are included here because of their dominance in the broad-sclerophyll forests.

THE CHAPARRAL ELEMENT

A considerable number of the Pliocene species are closely related to living species of the Climax Chaparral, a decidedly xerophytic association of the Sonoran life zone of the Coast Ranges and Sierra Nevada foothills. Its range is practically coextensive with that of the

broad-sclerophyll forest, which it virtually replaces in the lower altitudes of the southern Coast Ranges and southern Sierra Nevada. Its continuity as a dominant plant community is broken in the central Coast Ranges by the appearance of the broad-sclerophyll elements, which gradually replace the chaparral species further northward. In the northern portion of its range the chaparral overlaps vertically upward into the broad-sclerophyll forest. In the southern portions of both the Coast Ranges and the Sierra Nevada it overlaps upward into the conifer forests, with the intervention of only a few of the more xerophytic species of the broad-sclerophyll forest. At its lower limits the chaparral merges gradually into the dry grass-lands or coastal sagebrush. Throughout its entire range the chaparral is associated with typical riparian elements along the stream courses, though these are more common in its southern range, since northward these riparian species are gradually replaced by the more mesophytic of the broad-sclerophyll species and by redwood associates.

Fossil species:

Quercus orindensis Dorf
Heteromeles sp.
Cercocarpus cuneatus Dorf
Rhus sp.
Prunus merriami Knowlton
Garrya masoni Dorf
Pinus pieperi Dorf
Amelanchier sp.
Ceanothus chaneyi Dorf

Living species:

Quercus douglasii H. & A.
Heteromeles arbutifolia (Poir) Roem.
Cercocarpus betuloides Nutt.
Rhus laurina Nutt.
Prunus demissa (Nutt.) Walp.
Garrya fremontii Torr.
Pinus sabiniana Dougl.
Amelanchier alnifolia Nutt.
Ceanothus integerrimus H. & A.

Although conifers are not usually included in the term "chaparral," *Pinus sabiniana* is included here because of its intimate association with chaparral species, particularly *Quercus douglasii*, in situations where the chaparral merges into dry, open grasslands.

THE RIPARIAN ELEMENT

The Riparian, or stream-bank, element is by far the most important one represented in the Pliocene floras, when considered from the standpoint of the total number of species, their distribution among the various localities, and the actual number of specimens of each species at the individual localities. As previously pointed out (footnote, page 24) the term Riparian is here used to include only that association of stream-bank species which is intimately associated with the xerophytic grassland, chaparral, and several broad-sclerophyll species and conifers in the Sonoran life zone of the southern Coast Ranges and interior valleys. The association is typically developed in the semi-arid lowlands of southern California, where it depends chiefly on the moisture derived from the soil bordering the streams. It is dominated by *Platanus racemosa* Nutt., *Alnus rhombifolia* Nutt., *Populus trichocarpa* Torr. and Gray, *Salix lasiolepis* Benth., and other willows, *Juglans californica* S. Wats., and *Fraxinus oregona*

Nutt. From the coastal to the interior lowlands a few of these species, particularly of *Populus* and *Salix*, are replaced by other species of somewhat more xerophytic tendencies.

In the southern Coast Ranges the stream-bank element constitutes the only arboreal growth in the lower altitudes, the surrounding dry slopes supporting mainly species of the dry chaparral. At higher elevations competition arises with the more xerophytic of the broad-sclerophyll species, and still higher with the coniferous elements of the Transition zone. These same gradations are noted in passing from the southern to the northern Coast Ranges; from an almost exclusive association with chaparral species in the south, the riparian species become mingled with more and more of the broad-sclerophyll forest species, and locally with a few of the redwood elements, until in the central and northern Coast Ranges the stream-bank situations have become almost entirely occupied by such species, with the chaparral species confined to the open slopes. This reduction in the southern riparian element continues toward the north until in the redwood forest the stream-bank situations have been taken over almost completely by the more mesophytic of the broad-sclerophyll species and by typical redwood species. In the lower altitudes of the Sierra Nevada the riparian species again occupy the stream-banks in the dry, chaparral-covered foothills, gradually giving way upward to the coniferous and few broad-sclerophyll elements of the Transition zone. In the grassland areas of the interior valleys the riparian species constitute the only arboreal vegetation, ranging upward into the chaparral.

The distribution and associations of the Riparian element are of utmost importance to the later discussion of the separate localities and form the basis of the comparison of the Pliocene flora with that of today.

Fossil species:

Populus alexanderi Dorf
Salix coalingensis Dorf
Platanus paucidentata Dorf
Alnus merriami Dorf
Fraxinus caudata Dorf
Populus fremontii Dorf
Salix sp.

Living species:

Populus trichocarpa Torr. & Gray.
Salix lasiolepis Benth.
Platanus racemosa Nutt.
Alnus rhombifolia Nutt.
Fraxinus oregona Nutt.
Populus fremontii Wats.
Salix exigua Nutt.

THE EXOTIC ELEMENT

The number of Pliocene species which are not closely related to modern species of the California forests is rather small, as is to be expected in a flora of so recent an epoch of the Tertiary. Throughout the older Tertiary floras of the west there have been a considerable number of genera which have gradually been forced out of the Pacific region, possibly because of climatic and physiographic changes, and of competition with more adaptable forms. Other genera have

given rise in the more recent epochs to different groups of species than formerly existed, as is evidently the case in the prevalent live-oak group of the Pacific coast. Of the following species, two belong to genera no longer represented in California and one belongs to a group of oaks which has been relegated to a more southerly position.

Fossil species:

Ilex sonomensis Dorf
Ulmus brownellii Lesq.
Quercus bockéi Dorf

Living species:

Ilex brandegeana Loes. (Mexico.)
Ulmus parvifolia Jacq. (Asia.)
Quercus galeottii Mart. (Mexico.)

Very little information has been available concerning the ecological requirements of the Mexican elements. The temperate genera in the Central American areas are generally confined to the more xerophytic situations, leaving the mesophytic habitats to be occupied by the tropical genera.¹ Both *Ilex brandegeana* and *Quercus galeottii* are commonly associated with pines, firs and live-oaks in the dryer uplands. Such an association suggests an ecological similarity to the Broad-sclerophyll element discussed above. The xerophytic nature of *Ulmus parvifolia* has already been amply discussed by Chaney.² Since all of the species are of very restricted occurrence in the Pliocene deposits, their significance will be taken up in the later discussion of the individual floras in which they are found.

QUANTITATIVE CONSIDERATIONS

Whereas table 2 and table 3 clearly indicate the relative importance of each of the various elements represented in the Pliocene floras, additional information is obtained from a consideration of the actual number of specimens of each species collected. From such data is derived the percentage of both species and elements represented in each of the localities and in the flora as a whole.

A total of 1402 specimens has been counted from twelve localities. The remaining four localities have been omitted from any quantitative consideration on account of the small number of specimens available. The counts on the collection from two localities were made in the field, while those on the collections from the remaining ten localities were made partly in the field and partly in the laboratory, where the larger rock slabs were split for additional specimens.

In only one of the localities, number 150, was the leaf-bearing rock available in such unlimited quantities as to make a leaf count on more than 500 specimens. While such a condition is perhaps more ideal for any quantitative considerations, it is not commonly found in the Pliocene. In all of the remaining localities, however, the collections represent all of the leaf-bearing rock which was practicably available at the time of the writer's visits, so that no appreciable error can be said to be due to selective collecting.

¹ Paul C. Standley, Field Museum, Chicago, Oral communication, Jan. 6, 1930.

² Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 113, 114, 1927.

It is obvious that the accuracy and significance of any such quantitative consideration is proportional to the size of the collections. Since most of the Pliocene counts are based on rather limited collections, the data derived therefrom are not to be regarded as definitely established relations of the Pliocene plants, but rather as a tentative, though at present rather definite, interpretation, subject to revision at a future date when larger collections may be available.

The results of the counts on the specimens from the twelve localities are shown in table 4. Only three of the species, which are

TABLE 4

Species	Petrified Forest				Bennett Valley		Santa Rosa		Garberville			
Locality	150		151		152		154		155		156	
	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.
Redwood Element:												
Sequoia langsdorffii...	61	9.75	80	74.77	2	6.90
Pseudotsuga sonomensis.....	28	4.47	3	10.34
Odostemon hollickii...	5	.80
Smilax sp.....	2	.32
Broad-sclerophyll Element:												
Castanopsis chrysophylloides.....	1	2.78	2	6.90
Quercus lakevillensis...	20	3.20	13	12.15
Quercus hannibali...
Quercus declinata...	1	2.78	9	31.03
Umbellularia oregonensis.....	27	4.31	14	13.08	2	4.00
Chaparral Element:												
Heteromeles sp.....	3	.48
Cercocarpus cuneatus.....
Rhus sp.....
Prunus merriami.....
Garrya masoni.....	1	2.78
Amelanchier sp.....
Ceanothus chaneyi.....
Quercus orindensis.....	3	10.34
Riparian Element:												
Populus alexanderi.....	12	33.33	2	6.90	6	12.00	8	4.73
Salix coalingensis.....	2	6.90	15	30.00	3	1.78
Platanus paucidentata.....	17	47.22	3	10.34	3	6.00	42	24.85
Alnus merriami.....	1	2.78	14	28.00	51	30.18
Fraxinus caudata.....	2	6.90	10	20.00	65	38.46
Populus prefremonthii.....	3	8.33
Salix sp.....
Sierra-Cascade Element:												
Pinus sp.....
Libocedrus sp.....
Ribes stanfordianum.....
Pteris calabazensis.....
Exotic Element:												
Ilex sonomensis.....	145	23.16	1	3.45
Ulmus brownellii.....
Quercus bockéi.....	385	53.51
Totals.....	626	100.00	107	100.00	36	100.00	29	100.00	50	100.00	169	100.00

recorded only from the localities where the number of available specimens was limited, are unrepresented. The localities are arranged as in the preceding tables, except for the shifting of the column for locality number 160 to the extreme right. This has been done because of the exceptional and unique character of its flora, as will be discussed below (see page 52). The percentages are carried to two places, except where the third place decimals have figured in raising the second place decimal to make the total for each locality 100 per cent.

TABLE 4 (Continued)

Lakeville		St. Mary's College		Lafayette Dam		Coalinga		Alturas		Calabazas Canyon			
158		162		163		164		165		160		Totals	
No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.
.....	143	7.62
.....	3	1.76	34	1.38
.....	5	.07
.....	2	.03
2	5.56	5	1.27
11	30.56	44	3.82
.....	11	28.95	42	24.56	53	4.46
.....	10	2.82
5	13.89	48	2.94
.....	3	.04
.....	2	1.17	2	.10
.....	4	10.53	3	7.14	7	1.47
.....	2	5.26	3	7.14	1	.59	6	1.08
.....	4	5.56	5	.70
.....	9	5.26	9	.44
.....	10	5.85	10	.49
.....	7	18.43	1	2.38	2	2.78	13	2.82
.....	3	7.89	4	9.53	3	4.17	17	65.38	8	4.68	63	12.39
1	2.78	2	5.26	5	11.90	32	44.44	9	34.62	31	18.13	100	12.98
13	36.10	3	7.89	10	23.81	25	34.72	116	15.91
1	2.78	7	4.09	74	5.65
.....	3	7.14	6	8.33	86	6.74
3	8.33	2	5.26	2	4.76	10	2.22
.....	4	10.53	7	16.67	12	7.02	23	2.85
.....	4	2.34	4	.19
.....	4	2.34	4	.19
.....	27	15.78	27	1.32
.....	11	6.43	11	.54
.....	146	2.22
.....	4	9.53	4	.79
.....	335	4.46
36	100.00	38	100.00	42	100.00	72	100.00	26	100.00	171	100.00	1402	100.00

It is significant to note that the total percentages tend to further accentuate the importance of the Riparian element in the Pliocene floras. In the following list of the species which are represented by more than 5 per cent, 5 of the 6 are of the Riparian element.

<i>Platanus paucidentata</i>	15.91 p. ct.
<i>Salix coalingsensis</i>	12.98
<i>Populus alexanderi</i>	12.39
<i>Sequoia langsdorffii</i>	7.62
<i>Fraxinus caudata</i>	6.74
<i>Alnus merriami</i>	5.65

All five of the riparian species are seen to be consistently present at most of the localities. The high percentage of *Sequoia langsdorffii*, on the other hand, is primarily due to its abundance at one locality, rather than to an even distribution throughout the entire series. Of the remaining 25 species, represented by less than 5 per cent, 14 constitute more than 1 per cent and 11 less than 1 per cent. The complete discussion and interpretation of the quantitative data will be considered below in the section on the physical indications of the floras.

PHYSICAL CONDITIONS INDICATED BY THE FLORAS

COMPARATIVE RELATIONS OF PLIOCENE AND MODERN ELEMENTS

In an attempt to portray as accurately as possible the physical conditions which obtained in California during the Pliocene, comparisons will first be made between the relations of the Pliocene associations to each other and the corresponding relations of modern associations. It is obvious that the completeness of such a discussion is limited by the number of fossil plant species encountered in each of the elements. Conditions for the preservation of remains of all the species in any forest would be most unusual. By the study of the associations of which certain species are characteristic, however, it is possible to ascertain the type of forest growth which each species or group of species represents in spite of the incompleteness of the record.

In the preceding discussion of the composition of the Pliocene flora as a whole it is evident that the associations are primarily Californian in aspect. Tables 3 and 4 clearly indicate that the Riparian element is by far the most important in most of the formations. In the following discussion we shall concern ourselves mainly with the mixture of other elements with this Riparian element, as indicative of the conditions which existed in the vicinity of the particular localities at which the plants were collected.

The modern Riparian element represents an association which is typically developed in the southern less-mesophytic portions of California, decreasing in importance toward the northern, mesophytic forests, and increasing in importance, in fact becoming the only true arboreal growth, toward the interior valley grasslands. If the

Pliocene Riparian element is truly to be compared with the modern association, such relations should also be apparent in the study of the various Pliocene floras.

Table 5, based on the quantitative data of table 4, shows the total percentages of each of the elements, arranged according to the relative

TABLE 5

Localities	Elements					
	Redwood	Broad-sclerophyll	Chaparral	Riparian	Sierra-Cascade	Exotic
151	74.77	25.23
150	15.34	7.51	0.48	76.67
154	17.24	37.93	10.34	31.04	3.45
162	28.95	34.22	36.83
153	50.01	49.99
163	16.66	73.81	9.53
152	5.56	2.78	91.66
164	8.34	91.66
155	4.00	96.00
156	100.00
165	100.00
160	1.76	24.56	12.87	33.92	26.89
Average percentages	9.10	15.31	7.14	58.74	2.24	7.47

importance of the Riparian element at each of the localities. As in the previous table, locality 160 is relegated to a position at the end of the table because of the exceptional character of its flora, which will be discussed separately below. While certain general relationships are at once apparent, it must be remembered that the division of the floras into elements is made on a somewhat artificial basis, which neglects the fact that the corresponding elements in modern associations are not so easily delimited, since overlapping occurs between each of them where transitional conditions exist, and many species are common, though not dominant, in two or even more of the elements. With this in mind, we may regard the data shown in the table as expressions of general trends in each of the elements, rather than as constant mathematical percentages.

The Riparian element may be seen to increase in importance as the more mesophytic Redwood and Broad-sclerophyll elements decrease, representing the same inverse relationship as is prevalent in the modern forests. At the localities in the outer Coast Ranges north of San Francisco Bay, numbers 151 and 150 represent associations of redwoods and broad-sclerophylls, to the practical exclusion of the more xerophytic chaparral and the riparian species. Locality 154 in the same general region shows an increase in the riparian and chaparral

ral species, with the redwoods and broad-sclerophyll species still maintaining a position of dominancy. At the localities farther south in the outer Coast Ranges and both north and south in the inner Coast Ranges the redwood and broad-sclerophyll species become less and less important as the riparian species assume the rôle of dominancy, exactly as is to be expected from the comparison with the corresponding elements in the modern flora.

Closer comparisons of each of the Pliocene elements with its corresponding modern element tend to bring out other striking similarities between the past and present tendencies of the various associations. In the Redwood element the proportional decrease is rather constant from the localities in the outer Coast Ranges north of San Francisco Bay to those of the inner Coast Ranges of both the northern and southern portion of the state. The Broad-sclerophyll element exhibits a tendency to increase in importance as the redwood species decrease; it reaches its peak in locality 158 in the outer Coast Ranges, and becomes insignificant or absent in the inner Coast Ranges, Great Valley and interior ranges. The Chaparral element rises from complete absence or relative unimportance at the localities in the outer Coast Ranges north of the bay to its maximum development in the inner ranges east of the bay, steadily decreasing thereafter to insignificance or absence again toward the interior. The figures for the Riparian element, previously arranged in order of increasing percentages, indicate a steady rise from absence in the localities where the redwood species are dominant to increasing importance in the central, outer ranges and inner ranges, and finally to complete control in the Great Valley and interior ranges.

A consideration of a similar nature for the corresponding elements in the modern forests of California presents a striking comparison. In the outer Coast Ranges of the northern and central portions of the state the mesophytic Redwood element dominates the humid Coast Range or Redwood Forest. Southward and eastward the Broad-sclerophyll element, representing the degree of mesophytism between the conifer forests and chaparral, gradually becomes more and more prevalent in the border zones of the Redwood Forest. Still further southward and eastward the Redwood element disappears and broad-sclerophyll and chaparral species become the dominant forest cover in association with the Riparian element, which is confined to the stream-bank situations. In the southernmost coastal mountains and the inner Coast Ranges and valleys the Broad-sclerophyll element loses its position of dominancy to the Chaparral element, and the Riparian element becomes the only arboreal vegetation. Finally in the Great Valley the chaparral species are replaced by

grasses, and the fringes of trees along the stream valleys are almost exclusively made up of species of the Riparian element.

COMPARATIVE DISTRIBUTION OF PLIOCENE AND MODERN ELEMENTS

While the foregoing discussion brings out the general similarities between the Pliocene elements and their corresponding modern elements in the flora of California, more detailed information with respect to the past and present distribution of the various elements and species must be utilized before specific inferences can be made in regard to the physical conditions under which the Pliocene floras grew. Each of the individual floras will be considered separately in the comparison of the Pliocene and modern distribution of their various elements, as well as of their component species.

The absence or abundance of any one species at a locality is primarily to be regarded as an index to its absence or dominance in the forest growth which existed in that vicinity during any given period, although this may, indeed, not have been the case, since there are at least five contributing factors which should be considered: "(1) the distance of the given species from the stream, lake, or other site of deposition of sediments in which the leaves were buried, (2) the original thickness of the leaf, determining its ability to be transported without destruction, (3) the size and shape of the leaf as related to its transportation in the air and the water, (4) the habits of the plant with regard to shedding its leaves, and (5) the height of the stem of the plant, involving its arborescent, shrubby, or herbaceous habit."¹ A careful consideration of these factors is of much significance to the study of the Pliocene plant associations, particularly in the interpretation of the quantitative data of table 4.

SONOMA FLORA

The Sonoma tuff flora, which is centrally located with respect to the remaining floras, may be used as a basis for the distributional considerations. This flora comprises the collections from localities 150, 151, 152, 153 and 154, which are situated within a radius of 10 miles in the Coast Ranges east of the Santa Rosa valley and about 50 miles north of San Francisco Bay. Twenty species, representing over 57 per cent of the total Pliocene species, have been collected from these localities. Table 6 shows the total percentages of the species and elements, as well as the correlative species in the modern flora.

The total percentages of the elements indicate that the flora as a whole represents a forest dominated by the Riparian element, represented by 30.69 per cent, but in which the Redwood and Broad-sclerophyll elements, with totals of 26.83 and 19.06 per cent respec-

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. I, 11, 1925.

TABLE 6

Fossil species	Modern related species	Percentage by species	Percentage by elements
Redwood Element:			
<i>Sequoia langsdorffii</i>	<i>Sequoia sempervirens</i>	22.85	
<i>Pseudotsuga sonomensis</i>	<i>Pseudotsuga taxifolia</i>	3.70	
<i>Woodwardia bennetti</i>	<i>Woodwardia radicans</i>	*	
<i>Odostemon hollicki</i>	<i>Odostemon aquifolium</i>	.20	
<i>Smilax</i> sp.	<i>Smilax californica</i>	.08	26.83
Broad-sclerophyll Element:			
<i>Castanopsis chrysophylloides</i>	<i>Castanopsis chrysophylla</i>	2.42	
<i>Quercus lakevillensis</i>	<i>Quercus agrifolia</i>	3.84	
<i>Quercus declinata</i>	<i>Quercus tomentella</i>	8.45	
<i>Umbellularia oregonensis</i> ...	<i>Umbellularia californica</i>	4.35	19.06
Chaparral Element:			
<i>Heteromeles</i> sp.	<i>Heteromeles arbutifolia</i>	.12	
<i>Garrya masoni</i>	<i>Garrya elliptica</i>	.69	
<i>Quercus orindensis</i>	<i>Quercus douglasii</i>	2.58	3.39
Riparian Element:			
<i>Populus alexanderi</i>	<i>Populus trichocarpa</i>	10.06	
<i>Salix coalingensis</i>	<i>Salix lasiolepis</i>	1.73	
<i>Platanus paucidentata</i>	<i>Platanus racemosa</i>	14.39	
<i>Alnus merriami</i>	<i>Alnus rhombifolia</i>	.70	
<i>Fraxinus caudata</i>	<i>Fraxinus oregona</i>	1.73	
<i>Populus prefremontii</i>	<i>Populus fremontii</i>	2.08	30.69
Exotic Element:			
<i>Ilex sonomensis</i>	<i>Ilex brandegeana</i>	6.65	
<i>Quercus bockéi</i>	<i>Quercus galeottii</i>	13.38	20.03
Totals	100.00	100.00

* Represented by only a single specimen from Locality 153, from which a total of only three specimens was collected.

tively, are also important constituents. The Chaparral element is relatively unimportant. If the Exotic element, represented by 20.03 per cent, were properly placed with respect to the Californian elements, it would change the proportions considerably. Since the association in which *Ilex brandegeana* and *Quercus galeottii* are found in Mexico is ecologically very similar to the Californian broad-sclerophyll forest (see page 31), it would be reasonable to include these species in the Broad-sclerophyll element, in which case its percentage would increase to 39.09 per cent, a position of dominance over the Riparian element.

The foregoing percentages indicate conditions transitional between the modern broad-sclerophyll forests of the central and southern Coast Ranges and the redwood forest of the northern Coast Ranges. In considering such a border character for the flora, it is essential to distinguish between a marginal flora within the Redwood Belt and one on its southern end. Within the Redwood Belt the border character is due primarily to local topographic factors; at its southern end it is mainly climatic. In order to ascertain which of these border

forms is evident in the Sonoma flora we must consider each of the elements more closely.

The Redwood element, represented by five species, is notably lacking in the more typical redwood associates. *Acer macrophyllum*, *A. circinatum*, *Cornus nuttallii*, *Corylus rostrata californica*, *Rhododendron occidentale*, *Myrica californica*, *Arbutus menziesii* and *Rhamnus purshiana* are all unrepresented, in spite of their common occurrence in the modern redwood forest or its included border forests. Their absence can not be accounted for by any of the factors listed on page 37, since they are all arboreal, large or thick leaved, and favorably situated in relation to basins of deposition. In addition, the actual number of specimens of the species in the Redwood element, as listed in table 4, is exceedingly small at most of the localities. It is true that *Sequoia langsdorfii* is abundant at two localities, and *Pseudotsuga sonomensis* at one; both these occurrences, however, are at localities where the collections were large and contained a relatively small percentage of the same two species in contrast to the more xerophytic types. At the remaining localities the species of the Redwood element are exceedingly rare or absent. It must be added that while *Pseudotsuga taxifolia*, *Woodwardia radicans*, *Odostemon aquifolium* and *Smilax californica* are present in the Redwood Belt, they are by no means limited to it, so that the presence of their equivalents in the Sonoma flora is not necessarily indicative of conditions comparable to the humid Redwood Belt, but may merely verify the evidence of the presence of *Sequoia langsdorfii*, that at least local situations must have existed where conditions were suitable for scattered groves of redwoods and their hardier associates. On the whole, the consideration of the Redwood element is hardly conducive to an assumption of more than a limited growth of redwood forest types.

The evidence of the remaining elements lends weight to the intimation that the flora represents a border forest of the extremities of the Redwood Belt rather than within it. The Riparian element; represented by six species, has already been mentioned as of primary importance. In the present flora of California, the corresponding stream-bank species constitute an important element in both the broad-sclerophyll forests and the chaparral of the central and southern Coast Ranges, but can not be defined as a unit in the humid Redwood Belt. From a mingling with chaparral species in the south, the riparian species maintain their stream-bank habitat into the broad-sclerophyll forests toward the north, but are gradually replaced in the more humid northern Coast Ranges by the more mesophytic of the redwood border species, and finally by the typical species of the redwood forest proper. In the Coast Ranges north of San Francisco

Bay, where the Sonoma tuff localities are situated, the Riparian element can not be recognized as a definite association although several of the species occur as scattered individuals. *Platanus racemosa*, whose Pliocene correlative *P. paucidentata* is the most abundant of the riparian species at the Sonoma localities, is totally absent in the northern Coast Ranges. *Populus fremontii*, represented by *P. prefremontii*, which is third in importance in the Sonoma flora, is exceedingly rare in the valleys just north of the bay and totally absent from the flora of the more northern Coast Ranges. In the southern ranges and valleys it is a common constituent of the well-defined Riparian element, in association with broad-sclerophyll and chaparral species. The combined evidence of the dominance of the Riparian element as a definite unit and the differences in the Sonoma and present distribution of its constituents seems to corroborate the suggestion made above that the flora represents a forest near the southern margin of the Redwood Belt.

The relative importance of the Riparian, Broad-sclerophyll and Chaparral elements in the Sonoma flora are also in agreement with such a situation. At the southern margin of the Redwood Belt today, redwoods and their associates are mingled with broad-sclerophyll and riparian species while the chaparral species are rare or confined to the dryer uplands where their leaves are less apt to enter the sedimentary record. It is also apparent that the species of the Broad-sclerophyll element show the least variation in their total percentages in the flora, whereas the greatest variation is in the Chaparral and Redwood elements. Since these figures denote the consistency of the species in both distribution and number of specimens encountered, they tend to strengthen the position of the broad-sclerophyll species in the flora, which is in accord with their dominant role in the community in question.

It seems reasonably clear from the evidence of the elements represented in the Sonoma flora that the association represents a border forest comparable to that which grows today at the southern margin of the Redwood Belt in the Coast Ranges south of San Francisco Bay. As a means of verifying such a conclusion, it is instructive to compare the flora with the community now living in that region of California.

The modern redwood, *Sequoia sempervirens*, reaches its southern limit in the Santa Cruz and Santa Lucia Mountains, south of San Francisco Bay. This region was visited by the writer during the summer of 1927. The characteristic species of the forests here, based

mainly on the detailed reports by Jepson¹ and Shreve² together with corresponding Sonoma tuff forms, are shown in table 7.

TABLE 7

Southern Redwood Border Forest	Sonoma Flora
<i>Sequoia sempervirens</i>	<i>Sequoia langsdorffii</i>
<i>Pseudotsuga taxifolia</i>	<i>Pseudotsuga sonomensis</i>
<i>Quercus (Lithocarpus) densiflora</i>	<i>Quercus boeckei</i>
<i>Quercus agrifolia</i>	<i>Quercus lakevillensis</i>
<i>Quercus wislizenii</i>	
<i>Quercus douglasii</i>	<i>Quercus orindensis</i>
<i>Arbutus menziesii</i>	
<i>Castanopsis chrysophylla</i> var. <i>minor</i>	<i>Castanopsis chrysophylloides</i>
<i>Platanus racemosa</i>	<i>Platanus paucidentata</i>
<i>Umbellularia californica</i>	<i>Umbellularia oregonensis</i>
<i>Acer macrophyllum</i>	
<i>Myrica californica</i>	
<i>Populus trichocarpa</i>	<i>Populus alexanderi</i>
<i>Salix lasiolepis</i>	<i>Salix coalingensis</i>
<i>Alnus rhombifolia</i>	<i>Alnus merriami</i>
<i>Fraxinus oregona</i>	<i>Fraxinus caudata</i>

The more common shrubs of the same region include *Vaccinium ovatum*, *Cornus glabrata*, *Holodiscus discolor*, *Sambucus glauca*, *Rhamnus californica*, *Garrya elliptica*, and *Heteromeles arbutifolia*; of these only the last two have corresponding species in the Sonoma flora: *Garrya masoni* and *Heteromeles* sp. It is probable that the relative scarcity of the leaves of shrubs is due to their distance from the streams, to the smaller number of leaves which grow on a shrub as compared to a tree, and to the shorter distance of the leaf of a shrub above the ground, a situation which reduces its chance of being widely disseminated by the wind after shedding.

A total of 14 of the 20 species of the Sonoma flora are represented by related species in the Santa Lucia Mountains. These same species are also those which are most commonly encountered at the localities, constituting 82.54 per cent of the total number of specimens collected. Of the 6 species which are not represented, 2 have a northern, mesophytic aspect, and 3 a southern, more xerophytic one; the last is of no particular significance, due to the very widespread distribution of its modern correlative. *Odostemon aquifolium*, representing the Sonoma species *O. hollicki*, is common in the Redwood Belt, particularly in the more open aspect of the forest; *Smilax californica*, representing *Smilax* sp., is restricted to the redwood forest and its border zones in the northern Coast Ranges. Of the southern types, *Ilex brandegeana*, representing *I. sonomensis*, is not found in California, but is restricted to Mexico, where it grows on the dryer hillsides associated with pines, firs and live-oaks; *Quercus tomentella*,

¹ Jepson, *Silva of California*, Mem. Univ. Calif., vol. 2, 130, 1910.

² Shreve, *Vegetation of a Coastal Mountain Range*, Ecology, vol. 8, 34, 1927.

representing *Q. declinata*, is confined to the islands off the coast of southern California, where it grows along streams with poplars, willows, live-oaks and chaparral species. *Populus fremontii*, representing *P. prefremontii*, is not commonly associated with the Redwood element, being typical of the dry, interior valleys of the southern Coast Ranges and Great Valley. *Woodwardia radicans*, representing *W. bennetti*, is widely distributed in the lower altitudes throughout California. In the present connection, it is significant to note that it is found in the San Bernardino Mountains of southern California in association with typical riparian and broad-sclerophyll species, equivalent to those of the Sonoma flora.¹ The southern, more xerophytic aspect of the Sonoma association is accentuated by the proportion of the northern to the southern types: the latter is represented by 17.18 per cent, in contrast to only 0.28 per cent of the former. Further corroborative evidence of such an aspect may be deduced from a consideration of those species which are present in the Santa Lucia forests, but absent from the Sonoma flora. Table 7 shows that *Arbutus menziesii*, *Acer macrophyllum* and *Myrica californica* are unrepresented by corresponding Pliocene species. These species are characteristic of the more-mesophytic portions of the broad-sclerophyll forests and are common associates of *Sequoia sempervirens* in the Redwood Belt of northwestern California. It is difficult to explain the absence of corresponding species from the Sonoma flora by any of the factors listed on page 37. The obvious conclusion is that the conditions under which the Sonoma flora grew were not mesophytic enough to support them.

All of the foregoing considerations indicate that the Sonoma flora grew under conditions simulating those of the southern margin of the Redwood Belt in the Santa Lucia Mountains, though differing somewhat in its tendency toward a more southern and more xerophytic aspect. The latter suggestion seems to indicate that in the progressive restriction of the Redwood Belt, due to environmental changes, the redwood and a few of its associates may have lingered on in a region of generally adverse conditions because of local factors favorable to a limited growth. The evidence of the Sonoma flora indicates conditions even more adverse than those which now obtain at the southern limit of the Redwood Belt.

The presence of the redwood in the Santa Lucia Mountains, in which the rainfall is insufficient for a normal redwood forest, is conditioned by local topography and summer fogs, which generally occur at elevations of 500 to 1500 feet.² The result is the restriction of the Redwood elements to scattered and limited groves, surrounded

¹ Parish, Plant World, vol. 20, 163, 1917.

² Shreve, Ecology, vol. 8, 31, 1927.

by the normal growth of chaparral, riparian and broad-sclerophyll species. Precisely such localization seems evident in the Sonoma flora. Table 3 and table 4 clearly show that localities 150 and 151, at which the sediments were subaerially deposited (see pages 9 and 10), are the richest in the species of the Redwood element and entirely lacking in those of the Riparian element, suggesting an upland grove of redwoods and associates. Localities 152, 153 and 154 have only a poor or no representation in the Redwood element and a dominance of the species of the Riparian element, suggesting a lowland, stream-bank situation, which is in accord with the sedimentary evidence of deposition along the lower courses of streams or their debouchures into a marine embayment.

Having established a close relationship between the Sonoma flora of the Santa Rosa region and the southern marginal forest of the Redwood Belt in the Santa Lucia Mountains, it will be desirable to compare the climatic conditions of the two regions in question. In general, the Coast Ranges north of San Francisco Bay have a rainfall of over 30 inches annually, while those south of the bay have between 10 and 30 inches.¹ Santa Rosa, situated in the Santa Rosa valley near the Sonoma localities, has a rainfall of 29.92 inches on a 28-year average;² Calistoga, at a higher elevation in the same region, has 36.68 inches on a 45-year average; the region of the Petrified Forest, near which two of the Sonoma localities are situated, is over 500 feet higher than Calistoga, so would undoubtedly show a rainfall of 40 inches or more if figures were available. In comparable situations in the Santa Lucia Mountains, Monterey, in the coastal lowlands, has a rainfall of 16.71 inches on a 68-year average, or 13.24 inches less than at Santa Rosa; San Luis Obispo, of a slightly higher altitude, has 20.38 inches on a 53-year average, or 16.3 inches less than at Calistoga; and Santa Margarita, considerably higher in elevation, has 28.41 inches on a 27-year average, or about 12 inches less than at the Petrified Forest. These figures indicate that the northern Coast Ranges in the vicinity of Santa Rosa have had an increase of about 14 inches in annual rainfall since the Sonoma epoch. Although temperature figures for comparable situations in the Santa Rosa and Santa Lucia regions are not available, those from Santa Rosa and San Luis Obispo indicate that the mean annual temperature is now slightly lower at the northern station.

The increase in rainfall and slight decrease in mean annual temperature since the Sonoma epoch has resulted in important changes in the forest growth now living in the Santa Rosa region. The more

¹ Cooper, Carnegie, Inst. Wash. Pub. No. 319, pl. 2, 1922.

² Unless otherwise specified, all data on modern climatic conditions is contained in Summary of Climatological Data by Sections; U. S. Weather Bur. Bull. W., Sections 13-16, 1926.

conspicuous members of the forests in the vicinity of the Petrified Forest are as follows:

<i>Sequoia sempervirens</i>	<i>Ceanothus thyrsiflorus</i>
<i>Pseudotsuga taxifolia</i>	<i>Quercus agrifolia</i>
<i>Corylus rostrata</i> var. <i>calif.</i>	<i>Alnus rubra</i>
<i>Arbutus menziesii</i>	<i>Acer macrophyllum</i>
<i>Umbellularia californica</i>	<i>Salix lasiolepis</i>
<i>Lithocarpus densiflora</i>	<i>Pteris aquilina</i>
<i>Rhododendron occidentale</i>	

While there are several species in common between this assemblage and the Sonoma flora, notable differences in general aspect are apparent from a comparison with table 6. The species of the mesophytic Redwood element are more abundant and grow along the stream-bank in situations comparable to those in which the Sonoma flora must have grown. If as luxuriant a growth of redwoods and associates had thrived during the Sonoma epoch, they would have occupied these same mesophytic situations and have left a greater representation in the sediments than was evidently the case. Equally conspicuous in similar situations in the modern forest are the more mesophytic forms of the Broad-sclerophyll element, which are absent from the Sonoma assemblage. The Riparian element, though represented by a few species, is inconspicuous and can not be defined as a unit, even at a lower elevation in the region today. Of particular significance is the absence of *Platanus racemosa* and *Quercus tomentella*, whose equivalents rank second and fifth in abundance in the Sonoma flora; neither of these species is found in any portion of the northern Coast Ranges today. Similarly, *Quercus douglasii* and *Populus fremontii*, whose equivalents are present in the Sonoma flora, are unrepresented in the modern flora and exceedingly rare in the northern Coast Ranges. It is evident that the increase in rainfall and decrease in mean annual temperature since the Sonoma epoch has changed the forest growth of the region from a southern semi-xerophytic to a northern, mesophytic type.

MERCED FLORA

The flora of the Merced sandstones consists of nine species collected from localities 158 and 159. Seven species from the Lakeville locality are listed in table 8 with their percentages in the flora as a whole.

All of the species listed are common to the Sonoma flora. This is to be expected from the stratigraphic occurrence of the plants in sandstones intercalated with the Sonoma tuffs. The absence of any representatives of the Redwood element indicates a more xerophytic assemblage than the Sonoma flora and suggests a situation somewhat south of the southern margin of the Redwood Belt. With the exception of *Castanopsis chrysophylloides*, whose modern relative is not abundant in the southern Coast Ranges, the living equivalents of the

remaining species are common at lower elevations on the coastal side of the Santa Lucia Mountains and of the Sierra Madre, further south. Aside from the importance of the Riparian element, which is a natural consequence of its habitat along the stream courses, where leaves are most apt to enter the sedimentary record, the percentage of *Quercus lakevillensis* and *Umbellularia oregonensis* is suggestive of the oak groves, particularly of *Quercus agrifolia*, in the coastal foothills of the southern Coast Ranges, where *Umbellularia californica* is a common associate, and the riparian species, including the modern equivalents of those listed above, are met with along streams.

TABLE 8

Fossil species	Percentage by species	Percentage by elements
<i>Broad-sclerophyll Element:</i>		
<i>Castanopsis chrysophylloides</i>	5.56	
<i>Quercus lakevillensis</i>	30.56	
<i>Umbellularia oregonensis</i>	13.89	50.01
<i>Riparian Element:</i>		
<i>Salix coalingensis</i>	2.78	
<i>Platanus paucidentata</i>	36.10	
<i>Alnus merriami</i>	2.78	
<i>Populus prefremontii</i>	8.33	49.99
Totals	100.00	100.00

The evidence of the flora, indicating a close relationship to the modern flora somewhat south of the southern margin of the Redwood Belt, is in accord with the geographical location of the Lakeville locality, 20 miles southeast of the Sonoma localities. The lowland valley character of the flora agrees with the sedimentary evidence of deposition at the mouths of streams.

Only two species, *Pseudotsuga sonomensis* and *Pinus masoni*, have been collected from the Merced sandstones at locality 159, on the coast south of San Francisco. *Pinus masoni* is of particular interest. The very closely related modern species, *P. muricata*, is restricted to a narrow coastal strip in the seaward ranges, from the northern part of Humboldt County¹ on the north to San Luis Obispo County and the coastal islands on the south. It often occurs in pure stands, but may be associated with *Pseudotsuga taxifolia*, *Sequoia sempervirens* and a few of the broad-sclerophylls. The Merced association is of a similar nature and suggests coastal conditions of deposition. It is significant to note that the Pliocene equivalent of *Pinus muricata* is restricted to the costal sediments at this locality and locality 161, indicating the same specific habitat requirements as its modern relative. More specific climatic inferences can not be made from so small a collection, since the Mussel Rock locality is too centrally located with respect to the wide distribution of both modern forms.

¹ Jepson, *Manual of the Flowering Plants of California*, 48, 1925.

WILDCAT FLORA

The Wildcat flora, from localities 155, 156 and 157, comprises eight species, which are listed in table 9 with their total percentages.

TABLE 9

Fossil species	Percentage by species	Percentage by elements
<i>Redwood Element:</i>		
<i>Sequoia langsdorffii</i>	*	
<i>Pseudotsuga sonomensis</i>	*	
<i>Broad-sclerophyll Element:</i>		
<i>Umbellularia oregonensis</i>	2.00	2.00
<i>Riparian Element:</i>		
<i>Populus alexanderi</i>	8.37	
<i>Salix coalingensis</i>	15.89	
<i>Platanus paucidentata</i>	15.42	
<i>Alnus merriami</i>	29.09	
<i>Fraxinus caudata</i>	29.23	98.00
Totals	100.00	100.00

* Represented only by petrified wood specimens from locality 157.

On the basis of this list, which is made up entirely of Sonoma species, including all of the characteristic forms, the Wildcat and Sonoma associations are clearly related, though there are notable differences in quantitative aspects. The poor representation of the Redwood element and the extraordinary development of the Riparian element, while resembling the border forest at the southern margin of the Redwood Belt, suggest interior rather than coastal conditions. The eastward slopes of the Santa Lucia and Santa Cruz Mountains are wooded mainly with scattered groves of live-oaks and other broad-sclerophylls, in addition to the riparian species along the stream banks and a scattered growth of chaparral on the drier slopes; the redwoods and associates are rare and confined to the higher elevations, where local conditions of rainfall and fog make possible a limited growth. If a marine embayment extended conditions of deposition into such an interior valley, as was precisely the case during the Pliocene (see text-figure 1, p. 47), it is doubtful if the species of the Redwood element would form a conspicuous part of the plant record, except, perhaps, by drift wood. In general, such conditions seem to have obtained in the valley of the Eel River during the Wildcat epoch of deposition. The absence of live-oaks and chaparral species may in part be explained by their situation away from the stream banks or embayments in which sediments were being deposited.

The Wildcat flora is of particular interest as an indication of widespread restriction of the redwood forest during the Pliocene. All of the localities are situated in the heart of the present Redwood Belt, in a region of high rainfall and low temperature range. It is instructive to compare the town of Shively, as representative of the Red-

wood Belt, with Jasper Ridge, on the eastern slope of the Santa Cruz Mountains, where Cooper¹ reports a scattered growth of redwoods in an association dominated by riparian and broad-sclerophyll species. Shively, which is situated on the lower course of the Eel River, not far from the Wildcat localities, has a rainfall of 54.13 inches on an 8-year average, as compared to Cooper's figure of 32 inches for Jasper Ridge. This difference of 22.13 inches, while corroborating the suggestion of the Sonoma and Merced floras of a widespread increase in rainfall since the Pliocene, is approximately 10 inches more than the difference noted in the Santa Rosa region. The paleogeographic map shows that while the Santa Rosa and Lakeville regions were coastal during the Merced epoch of deposition, the Eel River region, in which the Wildcat localities are situated, was a marine embayment to the

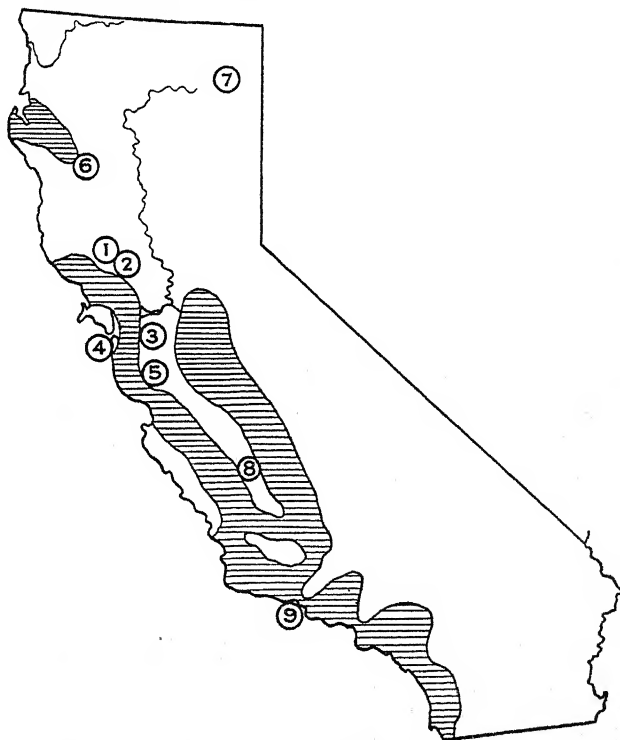


FIG. 1.—PLIOCENE PALEOGEOGRAPHIC MAP OF CALIFORNIA

Based on Clark's map (Jour. Geol., vol. 29, page 612, 1921), into which have been inserted locations of various Pliocene plant localities. In a recent communication Clark expressed the opinion that certain features of his map are incorrect as he now sees it. There was no marine embayment in vicinity of San Francisco Bay; instead, thousands of feet of land-laid deposits were being laid down in what Clark calls the San Ramon basin, which lay between the Merced embayments to the north and south.

In comparison of past and present distribution of various Pliocene plant associations, it is instructive to compare Pliocene locations of various localities with their present locations, as shown in plate 1.

¹ Cooper, Carnegie Inst. Wash. Pub. No. 319, 30, 1922.

east of the present Mendocina Range. Such a situation, with a topographic barrier to the west of it, would naturally have a lower rainfall than the coast regions west of the barrier. Comparable valleys of today have, as a rule, approximately 10 inches less rainfall than the corresponding coastal slopes; precisely the same relationships are apparent in the figures above.

There remains the possibility that the redwood forest may have been more prominent in the coastal region from which the Wildcat flora has been collected. If the Sonoma region were similar to the southern margin of the present Redwood Belt, the coastal slopes of the Eel River region, 110 miles to the north, should support a redwood forest such as exists today at a similar distance north of the Santa Lucia Mountains. The evidence for such an intimation is lacking at the present time, but is to be looked for in the Pliocene sediments of the coastal portions of northwestern California and western Oregon.

ORINDA FLORA

The collections from localities 162 and 163, in the Orinda formation, contain eleven species, which are listed with their percentages in table 10 below.

TABLE 10

Fossil species	Percentage by species	Percentage by elements
<i>Broad-sclerophyll Element:</i>		
<i>Quercus hannibali</i>	14.48	14.48
<i>Chaparral Element:</i>		
<i>Rhus</i> sp.	8.84	
<i>Prunus merriami</i>	6.20	
<i>Quercus orindensis</i>	10.40	25.44
<i>Riparian Element:</i>		
<i>Populus alexanderi</i>	8.71	
<i>Salix coalingensis</i>	8.58	
<i>Platanus paucidentata</i>	15.85	
<i>Fraxinus caudata</i>	3.57	
<i>Populus prefremontii</i>	5.01	
<i>Salix</i> sp.	13.60	55.32
<i>Exotic Element:</i>		
<i>Ulmus brownellii</i>	4.76	4.76
Totals	100.00	100.00

Six of the 11 species have been recorded from the Sonoma flora; these make up a total of 52.12 per cent of the total specimens collected and are among the more characteristic species of both floras. While the dominance of the Riparian element is similar to its development in the Sonoma, Merced and Wildcat floras, the absence of redwood species and of all but one of the broad-sclerophyll species, and a corresponding increase in chaparral species, suggests a more xerophytic assemblage than has previously been noted. This is in accord with the location of the Orinda localities 50 miles southeast

of the Sonoma localities and with the sedimentary evidence of fluvial deposition in an intermontane valley, where the annual rainfall under present-day conditions is usually about 10 inches less than on the seaward slopes.

A comparison of the Orinda flora with that now existing in the region shows that there is evidence, as before, of an increase in rainfall since the lower Pliocene. Notable differences are the dominance in the modern flora of the more mesophytic broad-sclerophyll species, such as *Umbellularia californica*, *Arbutus menziesii* and *Acer macrophyllum*, which do not have representatives in the Orinda flora, and the scarcity of *Platanus racemosa*, whose fossil equivalent, *P. paucidentata*, is the most abundant species in the collections. *Quercus chrysolepis* is unrepresented in the modern flora, while its Pliocene correlative, *Q. hannibali*, is second in abundance at the Orinda localities. *Salix exigua*, represented by the Orinda form, *Salix* sp., which is third in importance, is also lacking in the present flora. Moreover, the region supports a relict redwood forest on Grizzly Peak, east of Berkeley, although this is due mainly to local fog conditions rather than to the normal amount of rainfall necessary for the growth of *Sequoia sempervirens* and its mesophytic associates.

The general xerophytic aspect of the Orinda flora is strikingly similar to the association recorded from the inner valleys of the Sierra Madre of southern California,¹ where all of the species, with the exception of *Ulmus brownellii*, which has no generic representation in the flora of California, are represented by closely related modern species. Although several of the modern forms extend to the dry coastal valleys of the same region, two are confined to the interior: *Salix exigua* and *Populus fremontii*; and two are common in the interior and rare along the coast: *Quercus douglasii* and *Fraxinus oregona*.² It is significant to note that *Ulmus brownellii* is more closely related to the xerophytic Asiatic species, *U. parvifolia*, than to the mesophytic American form, *U. americana*.

The comparison of rainfall conditions of the valleys of the Sierra Madre with those of the hills surrounding the Orinda localities may be used as an index to the nature of the increase since the Orinda epoch. The former have an average rainfall of 12 to 15 inches;³ the latter 20 to 25 inches (Berkeley, west of the crest of the Berkeley Hills, 25.82 inches on a 35-year average; Walnut Creek, east of the crest, and less than 5 miles east of the Orinda localities, 20.43 inches on a 34-year average). These figures indicate the same general order of increase in rainfall since the lower Pliocene as those for the Sonoma,

¹ Harshberger, *Phytogeographic Survey of North America*, 269, 1911.

² Jepson, *Manual of the Flowering Plants of California*, pages 264, 268, 273, 759, 1925.

³ Abrams, N. Y. Bot. Gard., Bull. 6, 307, 1910.

Merced and Wildcat localities, and are additional proof for the postulated restriction of the redwood forest.

ETCHEGOIN FLORA

Six species, listed below in table 11 with their percentages in the flora, constitute the small but significant flora of the Etchegoin formation, collected at locality 164.

TABLE 11

Fossil species	Percentage by species	Percentage by elements
<i>Chaparral Element:</i>		
<i>Garrya masoni</i>	5.56	8.34
<i>Quercus orindensis</i>	2.78	
<i>Riparian Element:</i>		
<i>Populus alexanderi</i>	4.17	91.66
<i>Salix coalingensis</i>	44.44	
<i>Platanus paucidentata</i>	34.72	
<i>Fraxinus caudata</i>	8.33	
Totals	100.00	100.00

Comparing table 11 with table 6 shows that all of the species are common to the Sonoma flora. The percentages of the elements and species, however, are in striking contrast to the floras previously discussed. Both the Redwood and Broad-sclerophyll elements are unrepresented; the association of riparian and chaparral species clearly indicates conditions comparable to the sparsely-wooded stretches of the present-day foothills bordering the Great Valley. The high representation of the riparian species is in accord with their dominance in the modern flora and with their stream-bank habitat, where their leaves appear more likely to enter the sedimentary record than those of the chaparral species. The occurrence of such an association in fluviatile or temporary lake deposits in the Great Valley shows that the topographic barriers, which today result in the semi-arid conditions of the interior valleys, were in existence during the Etchegoin epoch.

While the general aspect and proportion of elements in the Etchegoin flora are similar to those of the modern assemblage, there are specific differences of significance. The modern equivalents of *Populus alexanderi*, *Quercus orindensis* and *Garrya masoni* (see pages 29, 30) are not found today in the Great Valley,¹ but are found associated in the coastal slopes and inner valleys of the southern Coast Ranges. The inference of a coastal rather than an interior aspect of the Etchegoin flora may be a reflection of conditions resulting from the marine embayment which extended into the lower

¹ Jepson, *Manual of the Flowering Plants of California*, pages 268, 273, 732, 1925.

portion of the Great Valley during this part of the Pliocene (see paleogeographic map). Aside from such specific effects, this embayment had no influence in producing a more mesophytic association than exists today in the Great Valley.

A small collection of leaf impressions from the Jacalitos formation of the Great Valley has recently been sent the writer by Dr. R. W. Chaney. Although it has not been possible to include this collection in the fuller consideration of the Pliocene floras, it is rather significant that the species are of the same types as found in the Etchegoin of the same region. The specimens, collected by Dr. Hubert G. Schenck of Leland Stanford Junior University, come from the base of the Jacalitos formation, exposed in Zapato Creek, Fresno County, in the northern half of Section 23, Township 22 south, Range 15 East. The following species have been recognized:

Salix coalingensis
Populus alexanderi

Quercus lakevillensis
Platanus ?

This association indicates the same interior conditions of growth as are evident in the Etchegoin flora and shows that the localized conditions of semi-aridity, resulting from topographic barriers to the west, have been in existence in the Great Valley at least since the Jacalitos formation was being deposited during the lower Pliocene.

It is not possible to determine whether the semi-arid aspect of the Etchegoin and Jacalitos floras was due entirely to physical barriers; part of it, no doubt, was a result of the widespread desiccation which is evident in the floras of the outer Coast Ranges. In the Great Valley today the vegetation is dependent mainly upon moisture derived from the soil bordering streams, rather than upon rainfall. It is doubtful whether an increase or decrease of 10 to 15 inches of rainfall in such a region, where the annual rainfall is at a minimum, would appreciably alter the vegetation. Not until a much greater change had occurred would the plant growth begin to take on a different aspect, *i. e.* of mesophytism following an increase or of xerophytism following a decrease in rainfall.

ALTURAS FLORA

The flora from locality 165, near Alturas, comprises only two species, *Populus alexanderi*, represented by 65.38 per cent, and *Salix coalingensis*, represented by the remaining 34.62 per cent; both are common to the Sonoma flora. Such an association is of particular significance in its relation to the other Pliocene localities. Like the Etchegoin flora it indicates that the Pliocene floras differed considerably in aspect, depending upon their situation near or away from the Pacific Coast. In so differing they clearly reflect the influence of the topographic barriers which were in existence in California at this

time. In the Alturas region today, the ranges to the west still cut off much of the moisture from the coast, resulting in the sparse arboreal growth in which the modern equivalents of the Alturas species, *Populus trichocarpa* and *Salix lasiolepis*, are prominent along the streams, where their leaves have the best chance for preservation in the sedimentary record.

Specific climatic inferences are difficult to make in so small a flora. If the collections represent the total flora of the region, they infer the existence of extensive grasslands, in which the arboreal growth is limited to but a few riparian species along the stream courses. In comparison with the Etchegoin flora they indicate still dryer conditions, simulating those which now exist in the areas east of the Pacific ranges and which the plant record shows have existed at least since the withdrawal of the Pliocene embayment from the Great Valley.

SANTA CLARA FLORA

The flora from the Santa Clara beds comprises fourteen species from locality 160 and three species from Hannibal's Portola locality.¹ Table 12 below indicates the percentages of each species and element in the collections which have been made.

TABLE 12

Fossil species	Percentage by species	Percentage by elements
<i>Redwood Element:</i>		
<i>Sequoia langsdorffii</i>	*	
<i>Pseudotsuga sonomensis</i>	1.76	1.76
<i>Broad-sclerophyll Element:</i>		
<i>Quercus hannibali</i>	24.56	
<i>Æsculus</i> sp.	*	
<i>Arbutus</i> sp.	*	24.56
<i>Chaparral Element:</i>		
<i>Cercocarpus cuneatus</i>	1.17	
<i>Prunus merriami</i>59	
<i>Amelanchier</i> sp.	5.26	
<i>Ceanothus chaneysii</i>	5.85	12.87
<i>Riparian Element:</i>		
<i>Populus alexanderi</i>	4.68	
<i>Salix coalingsensis</i>	18.13	
<i>Alnus merriami</i>	4.09	
<i>Salix</i> sp.	7.02	33.92
<i>Sierra-Cascade Element:</i>		
<i>Pinus</i> sp.	2.34	
<i>Libocedrus</i> sp.	2.34	
<i>Ribes stanfordianum</i>	15.78	
<i>Pteris calabazensis</i>	6.43	26.89
Totals	100.00	100.00

* Observed in Hannibal's collections from the Portola locality, from which no collections have been made by the writer.

¹Hannibal, Bull. Torrey Bot. Club, vol. 38, 335, 1911.

A comparison with table 6 shows that only 5 species are common to the Sonoma flora. Of the remaining 12 species, 3 are found in only one other formation, *i. e.*, the Orinda, while 9 species are restricted to the Santa Clara flora. Of the latter, all but one, *Pinus* sp., are without generic relations in any of the lower Pliocene localities, and all of them are much more closely related to modern species than to any previously recorded from the Tertiary. This is consistent with the reference of the beds to the late Pliocene on the basis of invertebrates and of its stratigraphic relations (see page 17). It must be noted, however, that the relation of the flora to the rest of the Pliocene floras is not as distant as might be intimated from a consideration of the individual species. Of the total of 17 species in the flora, those 8 which are common to the Sonoma and Orinda formations represent 60.83 per cent of the Santa Clara collections. The differences in general aspect of the flora are mainly due to the introduction of a new element, whose relationship to the other elements and to the modern forest associations must be considered in the determination of the physical conditions under which the flora grew.

Table 12 shows that the Sierra-Cascade element, which has not been evident in any of the other floras, holds an important position in the Santa Clara association, with a percentage of 26.89. This element today is characteristic of the Transition zone of the Sierra Nevada, at altitudes of 2500 to 6000 feet; toward the north it descends to lower altitudes and to the south ascends to somewhat higher elevations in the cross-ranges of southern California. In this zone the species of the Sierra-Cascade element are associated with several broad-sclerophyll species and a number of rather restricted chaparral species. In addition, the Redwood element is represented by *Pseudotsuga taxifolia* and the Big-Tree, *Sequoia gigantea*, and the Riparian element has modern counterparts in several widespread species which are common along stream banks. The high percentage of the Riparian element in the Santa Clara flora may be accounted for by its habitat near the sites of deposition. It is significant to note that *Platanus paucidentata*, the most widely distributed and most common of the riparian species in the lower Pliocene, is unrepresented in the Santa Clara beds. The modern equivalent, *P. racemosa*, is restricted to lower altitudes and is not found in the Sierra-Cascade forest. Likewise, *Populus fremontii* and *Fraxinus oregana*, whose Pliocene relatives are common in the Sonoma and related floras but absent in the Santa Clara, are not associated with the Sierra-Cascade forest, but are confined to the lower valleys and dry foothills. In contrast, the modern correlatives of *Salix coalingensis*, *Populus alexanderi* and *Alnus merriami*, which are abundant in

the Santa Clara flora, enjoy a wide altitudinal range and are among the common associates of the Sierra-Cascade species. *Salix lasiolepis* ranges from 10 to 5000 feet,¹ and *Populus trichocarpa* and *Alnus rhombifolia* from 0 to 8000 feet.² While such considerations are in accord with the montane aspect of the Santa Clara assemblage, more convincing evidence is seen in a detailed comparison with the common species of the Sierra-Cascade community, shown in table 13.

TABLE 13

Sierra-Cascade species	Related fossil species
<i>Pinus lambertiana</i>	<i>Pinus</i> sp.
<i>Pinus ponderosa</i>	
<i>Pinus jeffreyi</i>	
<i>Libocedrus decurrens</i>	<i>Libocedrus</i> sp.
<i>Abies concolor</i>	
<i>Pseudotsuga taxifolia</i>	<i>Pseudotsuga sonomensis</i>
<i>Sequoia gigantea</i>	<i>Sequoia langsdorffii</i>
<i>Ribes nevadense</i>	<i>Ribes stanfordianum</i>
<i>Cercocarpus betuloides</i>	<i>Cercocarpus cuneatus</i>
<i>Ceanothus integerrimus</i>	<i>Ceanothus chaneyi</i>
<i>Amelanchier alnifolia</i>	<i>Amelanchier</i> sp.
<i>Pteris aquilina</i>	<i>Pteris calabazensis</i>
<i>Quercus chrysolepis</i>	<i>Quercus hannibali</i>
<i>Æsculus californica</i>	<i>Æsculus</i> sp.
<i>Arbutus menziesii</i>	<i>Arbutus</i> sp.
<i>Prunus demissa</i>	<i>Prunus merriami</i>
<i>Populus trichocarpa</i>	<i>Populus alexanderi</i>
<i>Salix lasiolepis</i>	<i>Salix coalingsensis</i>
<i>Alnus rhombifolia</i>	<i>Alnus merriami</i>

This list indicates that sixteen of the seventeen Santa Clara species are represented by modern equivalents in the Sierra-Cascade forest. The scarcity of conifers in the Santa Clara beds is probably due largely to the habits of these genera in shedding their leaves a needle at a time. Single needles are not as well suited for transportation by air or water currents as are the broader dicotyledonous leaves. Cones would be more likely to occur in the record, though they are much less numerous on a tree than are the leaves, and would hence only infrequently be encountered in the sedimentary record.

The modern Sierra-Cascade forest thrives under conditions of 25 to 35 inches of yearly rainfall.³ The close resemblance of the Santa Clara association to this forest suggests a similar amount for the upper Pliocene and indicates more humid conditions than existed in the same region during the lower Pliocene. From its geographic position 70 miles south of the Santa Rosa region, which supported an association similar to the southern margin of the present Redwood

¹ Jepson, *Manual of the Flowering Plants of California*, 266, 1925.

² Jepson, *Silva of California*, 23, 1910.

³ Jepson, *Manual of the Flowering Plants of California*, 7, 1925.

Belt, it is unlikely that the Santa Clara region supported any of the redwood or broad-sclerophyll species during the lower Pliocene. In the upper Pliocene, however, under more humid conditions, the mesophytic forests of both Sierran and Coast Range aspects, evidently became widespread in areas which had previously supported xerophytic assemblages of chaparral, riparian, and a few hardier broad-sclerophyll species. The introduction of the Sierra-Cascade element into the late Tertiary floras of the Coast Ranges may have been a result of the retreat of the marine embayment from the Great Valley at the end of the Etchegoin epoch. This would have provided an easy route of migration of the Sierran species by way of the cross-ranges of southern California and have given them access to any portions of the Coast Ranges in which rainfall and temperature conditions were favorable.

The montane aspect of the Santa Clara flora is hardly consistent with its occurrence in fluvial or lake deposits of a lowland valley character. Growing normally at altitudes of 2500 to 6000 feet, most of the Sierra-Cascade species descend to considerably lower elevations toward the north. *Pinus lambertiana*, for example, ranges as low as 2000 feet in northern California¹ and *Libocedrus decurrens* occurs at 1000 feet.² In the southern Coast Ranges, in which the Santa Clara region is located, the Sierra-Cascade species are rare and restricted to much higher altitudes than is normally the case in the Sierra Nevada. It is possible that the growth of such montane species in lower altitudes during the upper Pliocene indicates a general cooling, effecting a range of the Sierra-Cascade forest in the southern Coast Ranges similar to that which it now has in the northern part of the state.

It is not possible to say whether the humid, cooler conditions suggested by the Santa Clara flora were of a widespread nature or were merely local conditions, resulting from submergence of previously uplifted tracts or the wearing down of physical barriers to rainfall. It is likely that the ranges to the west of the region, which today effectively prevent the moisture-laden clouds from crossing over into the inner valleys, may have been sufficiently low during the upper Pliocene to permit a greater rainfall in the interior than obtains there today. Such conditions, however, would be conducive to a general rise in temperature rather than a lowering, on account of the ameliorating effect of proximity to the Pacific Ocean. This suggests that the cooling, at least, was of a widespread nature, which is in accord with the general trend toward cooling at this time in the northern hemisphere, resulting in the Pleistocene epoch of glaciation.

¹ Sargent, *Forest Trees of the Pacific Slope*, 25, 1908.

² Mitchell, U. S. Dept. Agri., Bull. 604, 20, 1918.

PICO FLORA

The small collections from the Pico sandstone, at locality 161 in southern California, include only two species, *Pinus masoni* and *P. pieperi*. The significance of *Pinus masoni*, as indicative of coastal conditions of deposition, has already been mentioned in connection with its occurrence at locality 159. *Pinus pieperi*, which is restricted to the Pico locality, is closely related to the modern *P. sabiniana*, which occurs in the arid foothills of the Sierra Nevada and the inner valleys of the Coast Ranges. It is absent from the humid Redwood Belt, being more characteristic of the lower fringes of the chaparral, where it borders on the valley grasslands. In such situations it is commonly associated with the xerophytic *Quercus douglasii*, whose Pliocene equivalent, *Q. orindensis*, is of common occurrence in the lower Pliocene deposits to the north. The association of its equivalent, *Pinus pieperi*, with *P. masoni* suggests the existence of dry, open, semi-arid slopes along the Pliocene coast-line.

The relation of the Pico floras to the northern floras of lower Pliocene age is not so apparent from so small a number of species. While *Pinus pieperi* is confined to this single locality the presence of strikingly similar cones of *Pinus masoni* in the Pico and the Merced formations is suggestive of contemporaneity. On the climatic basis, however, the flora is distinctly indicative of the same semi-arid conditions which resulted in the widespread restriction of the Redwood Belt during the lower Pliocene.

RELATION OF PLIOCENE ENVIRONMENTS TO THOSE INDICATED BY
EARLIER TERTIARY FLORAS OF THE WEST

The physical conditions indicated by the earlier Tertiary floras of the west are in striking contrast to those suggested by the Pliocene floras. The widespread Mascall flora, recently discussed by Chaney,¹ is considered closely related to the oak-madrone forest of California, with an indicated rainfall of about 30 inches. The unity of the flora, as represented by collections from five of the western states, infers uniform climatic conditions over a wide area and a low relief, in which topographic conditions had no particular influence on the distribution of the vegetation. Such a conclusion is in accord with recent opinions, summarized by Reed,² based on petrographic criteria and the Miocene invertebrate and vertebrate faunas of California. The Pliocene floras, on the other hand, indicate a reduction in rainfall and a topographic control of vegetational distribution. The reduction in rainfall from the Miocene to the Pliocene epochs varies from about 10 inches along the coast to about 25

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 25, 1925.

² Reed, Amer. Assoc. Pet. Geol., Bull. 10, pt. I, 130, 1926.

inches in the interior. It is possible that if the Mascall flora were known from localities in the coastal regions, the influence of proximity to the Pacific Ocean might have been as evident in its effect toward increasing the rainfall as it was in the Pliocene, and still is in the present. The presence of mountain ranges in the Pliocene had the effect of producing a distribution of vegetation similar in general aspect to that which now obtains in California. No such effect was apparent in the distribution of the Mascall flora. At the Pitt River locality, for example, which is situated in the interior of northeastern California¹ not far from the Pliocene Alturas locality, a typical Mascall flora is present, including such mesophytic types as *Sequoia langsdorffii*, *Umbellularia* sp., *Alnus* sp. and *Juglans oregoniana*. In contrast, the Alturas flora comprises only 2 species, *Populus alexanderi* and *Salix coalingensis*, which are typical members of the Riparian element which is so well developed along the stream banks of the dry inner valleys of California and the Great Basin.

A comparison of the various elements represented in the Mascall and Pliocene floras shows that the mesophytic Redwood element was much more dominant and widespread during the Miocene than in any portion of the Pliocene. The xerophytic chaparral, which was well represented in the Pliocene, was decidedly unimportant in the Mascall. While the Riparian element was evident in the Mascall, it had not assumed the dominant position that it subsequently did in the Pliocene. On the basis of the proportion of riparian and redwood species alone, the difference between the Mascall and Pliocene environments is clearly shown. In the former the redwood species are decidedly dominant over the riparian species; in the latter floras the reverse is true, accentuating the change from rather humid to semi-arid conditions of growth.

Within the genera which are represented in both the Mascall and California Pliocene floras, there are notable differences in the modern relationships of certain species. The widespread *Platanus dissecta*, for example, is related in leaf characters to the mesophytic *P. occidentalis*, whereas the abundant Pliocene *P. paucidentata* shows definite affinities with *P. racemosa*, which is confined to semi-arid habitats. Another widespread Mascall species, *Ulmus californica* is represented among living relations by the mesophytic *U. americana*, while the Pliocene form, *U. brownellii*, is closely related to the xerophytic Asiatic species *U. parvifolia*. The Mascall *Quercus pseudolrata* represents the mesophytic broad-leaved oaks, which have no Pliocene representatives; in their place, the Pliocene comprises an abundance of xerophytic live-oaks.

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 32, 1925.

The presence of species of a more southern, warmer facies in the Mascall, and their scarcity in the writer's collections indicates cooler and more temperate conditions in the Pliocene. Such genera as *Celastrus*, *Magnolia* and *Liquidambar*, which are present in the Mascall and absent in the Pliocene, imply warmer temperatures than exist in the regions west of the Rocky Mountains today. Only a single genus, *Ilex*, in the Pliocene floras is unrepresented in equivalent latitudes on the west coast today, aside from the genus *Ulmus* mentioned above.

While it is apparent that the Pliocene environment was cooler, drier and more diversified than that which obtained in the Miocene, the contrast with the Oligocene conditions is even more impressive. Chaney has already contrasted the Bridge Creek and Mascall floras¹ as indicative of a restriction of the widespread Oligocene Redwood Forest and of a reduction of rainfall of about 10 inches from the Oligocene to the Miocene. In summary, it seems evident that the reduction of rainfall and the effect of cooling conditions and diversified relief since the Oligocene have resulted in a widespread restriction of the Redwood Forest and its mesophytic associates, a gradual elimination of sub-tropical and Asiatic elements from the floras of the west and a resultant deployment of the xerophytic chaparral and riparian species.

CORRELATION

Since the formations from which the plant remains have been collected have already been rather definitely referred to the Pliocene on the basis of both paleontologic and stratigraphic evidence (see section on Stratigraphic Occurrence of the Floras, pages 6 to 23), the problem of correlation is not of first importance at the present time. This is rather fortunate, in view of the previous lack of any considerable record of Pliocene floras in western North America, with which the writer's collections might have been compared. The value of the California floras is enhanced by their association with formations of rather definite age, particularly in the consideration of future collections whose age relations may not be so definitely known.

The post-Miocene age of the floras is corroborated by a consideration of the proportion of species which have previously been recorded in the Tertiary to those which have not. Of a total of 34 species, only 5 species, or 14.7 per cent, occur in earlier Tertiary floras. Their distribution is shown in Table 14:

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 43, 1925.

TABLE 14

Fossil species	Eocene		Oligocene		Miocene		
	Ft. Union	Kenai	Bridge Creek	British Columbia	Floris-sant	Mas-call	British Columbia
<i>Castanopsis chrysophylloides</i>	×
<i>Prunus merriami</i>	×	×
<i>Sequoia langsdorffii</i>	×	×	×	×	×	×
<i>Ulmus brownellii</i>	×	×
<i>Umbellularia oregonensis</i>	×	×

While two of these species are not known earlier than the Miocene, the remaining three have a much wider range, which depreciates from their correlation value. In addition, recent collections made by Kirkham from the Idaho beds, of probable earliest Pliocene or latest Miocene age,¹ include *Ulmus brownellii* in an association of species very similar in facies to those observed in the California Pliocene. It is obvious that the Pliocene age of the California floras can not be determined on the basis of such wide-ranging species, though a late Tertiary age is suggested from the prevalence of the forms in the later rather than the earlier epochs.

The remaining 29 species are peculiar to the floras which the writer has studied from the California region. Of the total number of species encountered, including the five widely ranging species above, 31, or approximately 91.2 per cent, have closely related species in the modern flora, which have previously been listed in the Qualitative Considerations of the Floras (pages 23 to 31). While in almost every case the resemblance is closer to the modern species than to any forms previously known, 16 species show varying degrees of relationship to other Tertiary and Quaternary forms,² listed in Table 15 below. This figure does not include the long-lived species listed in Table 14 above.

This compilation indicates that two species have affinities with Oligocene species, of which one ranges upward into the Miocene, 12 with Miocene species, and 2 with Pleistocene species which occur also in the Recent flora. Both of the Oligocene relatives are rather generalized types, whose specific characters are not particularly diagnostic. Of the 12 related Miocene species, 5 are restricted to the Auriferous Gravels, 1 to the Mascall, 1 to the Latah, 1 to the Florris-sant, and 1 to the Esmeralda; the remaining 4 are more widespread, particularly in the Latah, Mascall and Auriferous Gravels. The predominance of Auriferous Gravels species may be due to their closer

¹ Virgil R. D. Kirkham, Univ. Chicago, Oral communication, Jan. 17, 1930.

² A detailed consideration of the affinities of each of the species with both modern and fossil forms is given in the discussion of the individual species in the systematic portion of the present report, pages 67 to 107.

TABLE 15

TABLE 10

Fossil species	Related Tertiary and Quaternary Species	Oligocene	Miocene					Pleistocene	
		Crooked River Flora	Esmeralda Flora	Florissant Flora	Yellowstone Park Flora	Latah Flora	Mascall Flora	Auriferous Gravels Flora	Tar-Pit Floras
<i>Alnus merriami</i>	<i>Alnus corrollina</i>
<i>Ceanothus chaneyi</i>	<i>Ficus mense</i>
<i>Libocedrus</i> sp.	<i>Libocedrus decur- rens</i>
<i>Pinus masoni</i>	<i>Pinus muricata</i>
<i>Platanus pauciden- tata</i>	<i>Platanus dissecta</i>
<i>Populus alexanderi</i>	<i>Populus lindgreni</i>
<i>Pteris calabazensis</i>	<i>Pteris silvicola</i>
<i>Quercus bockei</i>	<i>Quercus nevadensis</i>
<i>Quercus declinata</i>	<i>Quercus boweniana</i>
<i>Quercus humibali</i>	<i>Quercus transgres- sus</i>
<i>Quercus lakevil- lensis</i>	<i>Quercus agrifolia</i>
<i>Quercus orindensis</i>	<i>Quercus cognatus</i>
<i>Rhus</i> sp.	<i>Chrysobalanus pol- lardiana</i>
<i>Ribes stanfordia- num</i>	<i>Ribes protomela- num</i>
<i>Salix coalingsensis</i>	<i>Salix californica</i>
<i>Smilax</i> sp.	<i>Smilax lamarensis</i>

proximity to the localities from which the writer's collections were made in California. While the problem of the age of the Auriferous Gravels has by no means been settled, Chaney has recently pointed out¹ the close relationship of the Table Mountain, Mount Diablo and Corral Hollow floras to the Mascall of Washington, Oregon, Idaho and Nevada. The floras from Chalk Bluffs and Independence Hill may probably be somewhat older. The Latah flora, originally referred to lower to middle Miocene,² has recently been considered upper Miocene,³ and is correlated with Esmeralda, Florissant and Mascall floras.

On the whole, the 16 species which are related to previously known Tertiary and Quaternary forms indicate a closer relationship to the upper Miocene forms than to any others, though none is specifically equivalent. The remaining 13 species are unrelated or but distantly related to any previously recorded fossil species and are very similar to modern species of the California forests. It seems evident that the aspect of the floras, intermediate between the western upper Miocene and modern floras, rather significantly corroborates their reference to the Pliocene.

The same age relationship is accentuated by the comparison of the genera which are represented in the writer's collections but are unrepresented in the modern flora of California, with similar exotic genera in the Miocene. In the Mascall floras, according to Chaney,⁴ there are 9 genera which are unrepresented in the present vegetation west of the Rocky Mountains: *Ginkgo*, *Carpinus*, *Ulmus*, *Liquidambar*, *Celastrus*, *Ficus*, *Magnolia*, *Laurus* and *Persea*. These represent 31 per cent of the total number of genera listed. This percentage would be lowered somewhat by a complete revision of the Mascall genera. Chaney has recently expressed the opinion⁵ that three of these genera, *Ficus*, *Laurus* and *Persea*, might better be referred to temperate genera of somewhat similar leaf characters. In the Latah floras, Berry has encountered⁶ 26 genera, or approximately 33 per cent of the total of 75, which do not now exist in western America. In contrast, only 2 exotic genera have been encountered in the writer's collections; these constitute only slightly over 11 per cent of the total genera represented. Such a contrast seems wholly in accord with the progressive exclusion of exotic genera from the west since the Miocene, and emphasizes again the intermediate aspect of the Pliocene floras between those of the Miocene and the present.

On the basis of the climatic conditions which the Pliocene floras infer, they seem wholly in accord with a general trend toward aridity in the Tertiary of the west.⁷ The reduction in rainfall which they

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 33, 34, 1925.

² Knowlton, U. S. Geol. Surv. Prof. Pap. 140, 23, 1926.

³ Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 234, 1929.

⁴ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 36, 1925.

⁵ Chaney, Written communication, Jan. 25, 1930.

⁶ Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 228, 1929.

⁷ Carnegie Inst. Wash. Pub. No. 349, pt. II, 46, 1925.

indicate is consistent with their reference to the post-Miocene. This is particularly evident in the floras from the inner Coast Ranges and interior valleys of California, although a reduction is also evident in the floras from the outer Coast Ranges. It is not possible to ascertain whether such a trend is due entirely to the erection of topographic barriers; secular changes of climate may have played a secondary role. If more were known of the Oligocene, Miocene and Pliocene vegetation along the western coastal regions, and if such regions could be definitely shown to be unaffected by any physical barriers to the west, it would be possible to deduce that any trend toward aridity, if expressed, were a result of secular changes. In the return of cooler and slightly more humid conditions in the latest Pliocene, for example, the Santa Clara flora might conclusively intimate secular changes if it occurred in sediments along the coast rather than in an interior valley, where the change might well have been a result of the removal of any appreciable range to the west.

It seems evident that the consideration of the floras, from both the standpoint of genera and species and of the physical conditions which they infer, is in harmony with their reference to the Pliocene. Since the collections have been made from eight different formations in California, it will be instructive to compare the individual floras in an attempt to indicate specific age relations which formations have toward one another. In many respects there is a considerable degree of unity to be observed in the floras; in other respects they differ considerably.

From the discussion concerning the physical conditions which the individual floras suggest, it is apparent that topographic conditions of relief had the same influence on the character and distribution of the Pliocene vegetation as it does in California today. On the basis of species alone it would be impossible to prove that the modern xerophytic associations of the interior valleys were contemporaneous with the mesophytic associations now growing in the humid coastal regions of northwestern California. In the former associations none of the mesophytic elements is present; in the latter, the xerophytic chaparral species and the riparian species are rare, but nevertheless present, in the more open aspects of the forest. In short, the most widespread species, and hence the most useful for correlation purposes, are those which are least sensitive to rainfall conditions. In the present forests of California, for example, the most widespread species, by means of which the mesophytic and xerophytic associations might well be shown as contemporaneous, are the riparian species, which are less restricted by rainfall than are any of the more mesophytic broad-sclerophylls or conifers.

The widespread distribution of the Riparian element and the restriction of the mesophytic Redwood element during the Pliocene has already been fully discussed (see pages 34 to 56). One could hardly be expected to use the Redwood element as a criterion for close correlation, any more than one could use it successfully today, on account of its sensitivity to atmospheric conditions and its consequent restricted distribution. Using the Riparian element as the index element for the floras of the Pliocene formations, they may be seen to be not only of the most widespread occurrence, but also of greatest abundance. Table 4, based on the localities from which appreciable collections have been made, indicates that *Populus alexanderi* and *Salix coalingensis* occur in 9 localities each, *Platanus paucidentata* in 8, and *Alnus merriami* and *Fraxinus caudata* in 5. These same 5 species, all characteristic members of the Riparian element, represent 53.67 per cent of all the specimens encountered.

While there is thus a reflection of unity among the floras of the Pliocene formations, a comparison of the total species from each of the formations indicates minor discrepancies of age significance. Using the flora from the Sonoma formation as a basis for such comparison, on account of the varied habitats recorded there and hence a fuller representation of the vegetation, the following table of percentages is derived:

TABLE 16

Formation	Number of species recorded	Species common to the Sonoma formation	
		Number of species	Per cent of total
Sonoma	20	20	100.00
Merced	9	8	88.89
Wildcat	8	8	100.00
Orinda	11	6	54.55
Etchegoin	6	6	100.00
Alturas	2	2	100.00
Santa Clara	17	5	29.41

The significance of such figures depends, naturally, upon the size of the collections. For this reason any age deductions on the two species from Alturas would seem hazardous. The greatest discrepancy is seen to occur in the Santa Clara formation. This is in accord with the late Pliocene age of the beds, based on stratigraphic and paleontologic methods, and also with the relation of its assemblage of species to the Pliocene floras and to the modern flora, as previously discussed on page 52. In the Orinda formation, while the discrepancy is not as great, it seems to indicate that the flora is not strictly contemporaneous with at least the Sonoma flora. Table 3 shows that 3 species, *Quercus hannibali*, *Prunus merriami* and *Salix*

sp., are common to the Santa Clara and the Orinda floras, suggesting that the Orinda flora, which otherwise is very closely related to the Sonoma flora, is nevertheless somewhat younger in age. The stratigraphic table verifies such a conclusion. The same table, however, shows that the Etchegoin formation is somewhat younger in age, on the basis of invertebrate collections, than the Sonoma and Merced, indicating the caution which must be exercised in floras of a limited number of species. The same holds true for the Pico formation, in which only 2 species occur. One of these, however, is common to the Merced and suggests a degree of contemporaneity.

The consideration of the exotic genera and species in the Pliocene floras may also be used as suggestions for age-relationship. The presence in a flora of genera which are not represented in the modern flora of the west, but which were widespread in earlier Tertiary periods, would be suggestive of earlier age than the floras in which such exotic genera were absent. The Sonoma flora, for example, has in it one exotic genus, *Ilex*, in addition to one species, *Quercus bockéi*, which is not closely related to any living California species. The Orinda flora contains leaves of the exotic genus *Ulmus*. In striking contrast, the Santa Clara flora does not comprise a single genus which is not present in the living flora of California. The difference suggests a younger age of the Santa Clara formation with respect to the former, particularly in view of the more detailed evidence given above.

The comparison of the Pliocene floras of California with other floras in the west, or elsewhere, has brought out rather significant observations. In a recent paper¹ on the study of petrified wood from the Ricardo tuffs of Pliocene age, situated in the El Paso Mountains of southeastern California, Mrs. Webber notes an association of pine, cypress, palm, live-oak and osage orange, representing a valley flora of a plains area of rather limited rainfall. Such a conclusion is in accord with the postulated reduced rainfall in California during the Pliocene, and offers a close comparison with the Etchegoin and Alturas floras of the interior, both of which indicate the existence of plains areas in which the vegetation was limited to riparian species along stream banks and a few xerophytic chaparral species.

There is reason to believe that the Esmeralda flora² of Nevada, which has recently been referred to the upper Miocene,³ may well be as young as the lower Pliocene. Berry's revision⁴ of the flora comprises 22 species, of which 16 are peculiar to the Esmeralda formation and 6 have previously been recorded from various Miocene floras, particularly the Payette. The latter do not seem particularly

¹ Webber Manuscript, Sept. 1929.

² Knowlton, U. S. Geol. Surv. 21st Ann. Rpt. 209, 1900.

³ Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 235, 1929.

⁴ Berry, U. S. Nat. Mus. Proc., vol. 72, art. 23, 1, 1928.

diagnostic in view of their being mainly generalized types, including two aquatics, *Typha lesquereuxi* Cockerell and *Trapa americana* Kn., and two willows, *Salix inquirenda* Kn. and *S. knowltoni* Berry. Of greater significance is the absence of conifers, notably *Sequoia langsdorffii*, the presence of three, and a questionable fourth, species of *Salix* and one of *Populus*, and the introduction of the chaparral type of oak, represented by *Quercus turneri* Kn. The whole assemblage seems to imply, as Berry has brought out, rather semi-arid conditions of growth. The Payette flora, on the other hand, includes such mesophytic types as *Sequoia langsdorffii*, *Umbellularia* sp., *Acer gigas* and *Ulmus californica*, none of which is present in the Esmeralda. The similarity of the environmental conditions which the Esmeralda and the California lower Pliocene floras indicate is suggestive of age equivalence. In this connection, it is significant that recent vertebrate collections from the Esmeralda indicate lower Pliocene rather than Miocene age, according to Matthew.¹

A recent list of species² submitted on the Kirkham collections from the Idaho beds likewise suggests a Pliocene rather than a Miocene assemblage. While this list of determinations, made by Berry, includes only one species, *Ulmus brownellii*, which is present in the Pliocene, the general aspect of the flora is similar to that noted in the floras from the inner valleys of California. It is possible that a closer comparison of the Idaho specimens with those from the Pliocene would indicate a larger number of common species. Notably absent from the Idaho flora are *Sequoia langsdorffii* and its mesophytic associates, mentioned above, which are consistently present in the Miocene floras of the west.³ The presence of one species of *Platanus*, two of *Salix*, and two and a questionable third of *Quercus*, suggests a scattered forest growth dominated by riparian species and oaks, such as is prevalent in several of the Pliocene floras. It seems significant that *Ulmus brownellii* is of the xerophytic Asiatic type,⁴ rather than related to the mesophytic American species. It is hoped that larger and more complete collections may be made from the Idaho beds to verify or contradict the inference made above.

An attempt has been made to correlate the Pliocene floras of California with those previously recorded from eastern America and Europe. The Citronelle flora⁵ of the Gulf States of America does not comprise any species with which the writer's species might be closely compared, indicating that the conditions which make the modern California flora peculiar to that region were effective during the Pliocene. The only basis on which a comparison can be made

¹ Matthew, Oral communication, Sept. 4, 1929.

² Virgil R. D. Kirkham, Oral communication, Jan. 5, 1930.

³ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 35, 1925.

⁴ See page 31.

⁵ Berry, U. S. Geol. Surv. Prof. Pap. 98, 193, 1917.

between the California and Citronelle Pliocene floras is on the similar relationship which each of the floras shows toward the forest growth existing today in the regions from which the collections were made. The relation of the California Pliocene floras to the European Pliocene is even less apparent.

SUMMARY

The Pliocene floras of California indicate a close relationship to the living forests of California in both general aspect and distribution, though they differ somewhat in details. The writer has encountered 34 species at 16 scattered localities throughout the state. From a consideration of their associations and distribution it is evident that conditions were unfavorable during the Pliocene for more than a restricted growth of Redwood Forest, which is in striking contrast to its widespread occurrence in the northern hemisphere during the Oligocene epoch and to its prevalence in western America during the Miocene. The effect on the forest growth of a reduction in rainfall and temperature from the Miocene to the Pliocene was accentuated by the influence of relatively high topographic relief in the region, which resulted in a distribution of vegetation similar to that which exists today in the coastal regions and inner valleys of California, where the plant associations are greatly affected by localized conditions of rainfall and relief. The Pliocene floras clearly indicate a change from comparatively uniform conditions during the Miocene to rather diversified conditions during the Pliocene.

The more detailed comparison of the Pliocene and modern forest indicates that the climatic conditions during the lower Pliocene were somewhat dryer and warmer than those existing in the same regions today. The effect was a greater restriction of the Redwood Belt than prevails in the living forests of California and an elimination of Tertiary types no longer living in western America. The upper Pliocene seems to have experienced a return of more humid and cooler conditions than obtain in comparable situations today, resulting in the reappearance of humid elements in regions where they had been absent during the lower Pliocene. At this same time the coastal ranges were invaded by a forest of Sierra Nevada aspect, as a result, no doubt, of the opening up of transverse paths of migration across the mountains of southern California.

There is little in common between the Pliocene floras of California and those of eastern America and Europe, except in their close relationship to the existing flora of the regions from which they were collected. Differences in species and general aspect between California and Eastern floras are similar to differences which now exist between these same regions, and are a reflection of the influences of long established climatic and physical barriers to intermigration.

SYSTEMATIC DESCRIPTIONS

The collections from the Pliocene formations of California include 34 species, all of which have been definitely referred to genera still living in North America. Eight species are not represented by material sufficiently well preserved to justify giving them specific names. Of the remaining 26 species, which are given specific names, 21 are here described as new and 5 as previously recorded in the Tertiary record of the west. The large number of new species is due to the fact that Pliocene floras have not previously been encountered in the west, except for small, scattered collections in which the specimens were poorly preserved or were referred to modern species. There remain two species which are mentioned in the discussion of the Santa Clara flora. These species, *Arbutus* sp. and *Æsculus* sp., are not included in the systematic descriptions because of their occurrence at the Portola locality, from which no collections have been made by the writer and because of the inadequate specimens by which they are represented.

In the final determination of genera and species, comparisons have been made with both fossil and living related species. Herbarium materials have been consulted at The New York Botanical Garden, The Field Museum of Chicago and the herbarium of the University of California. In most cases the species are more closely related to living species than to any previously recorded in the fossil record. The practise of referring fossil plants, particularly of which only the leaves are known, to living species seems rather hazardous in view of the difficulty with which the majority of modern species are differentiated on such limited portions of the plant as a whole. Unless more corroborative and diagnostic portions be found, the similarity in leaf form alone does not seem to justify the reference to a related living species. In every case, however, where the fossil leaf impressions are not distinguishable from modern forms, the close relationship of the Pliocene to the modern species is mentioned and stressed in the discussion.

PHYLUM PTERIDOPHYTA

ORDER FILICALES

Family POLYPODIACEÆ

Genus *PTERIS* Linné*Pteris calabazensis* Dorf, new species

(Plate 5, figs. 1, 2)

This genus is represented at only one locality, by two rather well-preserved specimens on a single slab of rock. The better of the two consists of a portion of a pinna 28 mm. long and 20 mm. wide, showing a slight tapering from bottom to top.

Description—Outline of frond unknown but at least pinnate and the pinnae pinnatifid; pinnae apparently long-lanceolate with a thin rachis, cut with numerous, separate, sub-opposite, narrowly lanceolate pinnules; individual pinnules sessile with entire or undulate margins, usually lobed at the base, diverging from the secondary rachis at very obtuse or right angles (80° to 90°); pinnules average 13 mm. in length and 5 to 7 mm. in width, the basal lobes increasing the width to 8 or 9 mm.; regularly spaced on the secondary rachis at intervals of 6 to 8 mm.; midrib of pinnules thin and arched slightly upward; veins fine, except the medial ones of the basal lobes, numerous (10 to 14 pairs), and branching dichotomously near the midrib, usually forking again before reaching the margin.

Discussion—Although hardly complete in all details, the two fragments of this species seem sufficiently well preserved to warrant specific determination. The generic reference is based wholly on comparisons with herbarium material of modern ferns of western North America. The best comparisons are with the numerous sheets of *Pteris* (*Pteridium*) *aquilina* L. var. *pubescens* and var. *lanuginosa* (Bory) Hook. at The New York Botanical Garden, especially those collected in the mountains of San Diego County and the San Bernardino Mountains, California.

Pteris calabazensis is quite unlike any of the figured Tertiary forms of this genus, of which only five are known. In three of these the pinnules are much longer and narrower; the fourth, *Pteris* sp., from the Latah Miocene,¹ is so incomplete that no comparison can be made; the last, the Crooked River Oligocene species, *Pteris silvicola* C. C. Hall,² a humid type with rounded or oblong pinnules, is perhaps the nearest Tertiary relative, as is suggested by its reference to the modern *P. aquilina*. *P. calabazensis* is also suggestive of *Dryopteris idahoensis* Knowlton³ from the Payette Miocene of Idaho, differing only in the doubly forked veins and the greater tendency toward entire rather than dissected pinnules.

This species is not common in the Pliocene deposits of California, due perhaps to its fragile nature or its distance from areas of deposition. Its similarity to the more xerophytic varieties of the modern *Pteris aquilina*, as well as its association with inhabitants of exposed situations, suggests that it grew like its modern equivalent on the dry upland slopes, where but few of its fronds would be likely to enter the sedimentary record.

Occurrence—Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 301, 302, Loc. 160.

Genus WOODWARDIA J. E. Smith

Woodwardia bennetti Dorf, new species

(Plate 5, fig. 3)

The fragment figured is the only one which has been found and is probably the basal or middle portion of a pinna. The venation is indistinct and the borders of the pinnules are slightly curled, obscuring any fine serrations which might be present. Enough of the general and specific details are present, however, to make a specific determination possible.

Description—Fronds probably at least pinnate and the pinnae pinnatifid; shape of pinnae evidently long and lanceolate; pinnules equal or sub-equal in both size and shape, sub-falcate, disjointed to almost their entire length,

¹ Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 237, 1929.

² Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 100, pl. 8, figs. 2, 4, 6, 7, 1927.

³ Knowlton, U. S. Geol. Surv., 18th Ann. Rept., pt. 3, 721, pl. 99, figs. 1, 2, 1898.

separated by long, narrow sinuses; narrowly lanceolate, apparently entire; length of pinnules 23 to 26 mm., width 7 to 8 mm. in the center, tapering gradually to broad, decurrent bases and acute points; midrib prominent, distinct to the points, curving slightly upward; secondary venation indistinct, yet showing clearly a row of long, narrow areoles on each side of and parallel to the midrib of the pinnules; outside of these the finer veins diverging obliquely from the borders of the areoles, anastomosing toward the margin, forming irregular meshes.

Discussion—Among modern ferns, *Woodwardia chamissoi* Brock. and *W. radicans* (L.), both of which are included under *W. spinulosa* Mart. et Gal. in the herbarium of The New York Botanical Garden, are most similar to the present species. The sterile pinnules of *W. radicans* in sheet No. 2270 are essentially similar in venation, texture, shape and size, differing only in having finely serrate margins, a feature which may have been present originally but subsequently obscured by the coarse preservation and the curled margins of our specimen.

There are but six described or figured species of *Woodwardia* recorded from the Tertiary of North America, two of which are comparable to the present species: namely, *W. latiloba* Lesquereux from the Denver Eocene of Colorado,¹ the pinnules of which are much shorter, wider and more obtuse, though the general characters are similar to those of our species; and *W. præradicans* Berry from the Latah Miocene,² which differs mainly in the size of the pinnules and the details of venation. In the European Tertiary the similarity to *W. radicans phiocenica* Sap. et Mar.³ is much more striking. The differences in venation and margin may be more apparent than real as both of these characters are rather poorly defined in *W. bennetti*.

The scarcity of this species in the Pliocene deposits of California can perhaps best be explained by the scarcity of most of the more humid types of plants, such as are now associated with the typical redwood forest. The association of the fossil species with *Sequoia langsdorfi* suggests that, like its modern equivalents, *Woodwardia radicans* and *W. chamissoi*, it grew in a habitat where moisture conditions were favorable enough for at least a scattered growth of redwoods, such as prevails today in the Coast Ranges south of San Francisco Bay.

Occurrence—Bennett Valley, Locality 153.

Collection—Univ. Calif. Coll. Pal. Bot., Holotype, No. 303, Loc. 153.

PHYLUM SPERMATOPHYTA

CLASS GYMNOSPERMÆ

ORDER CONIFERALES

Family PINACEÆ

Genus PINUS Linné

Pinus pieperi Dorf, new species

(Plate 5, figs. 7 to 10)

This species is represented by the carbonized basal portion of a pine cone with its top broken off abruptly and the terminal portion of a second

¹ Lesquereux, U. S. Geol. Surv. Terr., vol. 7, 54, pl. 3, figs. 1, 1a, 1878.

² Berry, U. S. Geol. Surv. Prof. Pap., 154-H, 236, pl. 64, figs. 22, 23, 1929.

³ Saporta et Marion, *Végétaux Fossiles de Meximieux*, 215, pl. 22, 1876.

cone in which both the scales and seeds are well preserved. Both specimens are slightly weathered and mutilated.

Description—Cone apparently large, probably 15 to 25 cm. long, the portions preserved suggesting an ovoid or sub-globose shape; scales more or less united at the base, separated at the apex, up to 4 cm. long, 1 to 2.5 cm. wide, ending in obliquely raised pyramidal spur-like projections, 10 to 25 mm. long; these terminal projections broken off at various distances above their bases, presenting rhomboidal cross-sections with sharp acute angles laterally, rounded obtuse angles above and below, and terminating laterally in a sharp ridge on each side of the spur; upper and lower sides of each prolongation marked by a central, longitudinal line. Seeds resting in deep hollows on the scales preserved in the terminal portion; 2 cm. long, oblong, flat and centrally grooved on the upper surface; seed-wings, of which a few remnants are preserved, short and encircling the seeds.

Discussion—This species is not comparable to any described or figured pines from the Tertiary of North America. Its preservation as carbonized fragments in a marine deposit is unique in itself for cones of Pliocene age.

Among living forms it is clearly of the type of *Pinus sabiniana* Dougl. or *P. coulteri* Don. of the west coast. Examination of cone material of these species at The New York Botanical Garden and at the University of California, indicated that both forms resemble the fossil in size, in the spur-like projections at the ends of their scales, and in their tendency to break off near the base when falling. However, the seeds of these pines are sufficiently different to indicate that *P. sabiniana* is the more closely related to the Pliocene species. The seeds of *Pinus coulteri* are globose, with a wing nearly twice as long as the seed, whereas those of *P. sabiniana* are oblong, slightly flattened and with a very short encircling wing. The seeds and wings of the fossil species are clearly of the *P. sabiniana* type (see plate 5, figs. 7, 8, 9).

Pinus sabiniana is common today in the dry valleys and foothills of California, in association with an open type of growth, such as chaparral and live oaks. It reaches the coast only in the Santa Lucia Mountains. The occurrence of the fossil species in a marine deposit directly on the present coastline suggests either a former marine embayment sheltered by ranges now eroded away or the occurrence of the species along the Pliocene coast under conditions similar or perhaps slightly more arid than they are today.

The species is named in honor of Mr. Harold K. Pieper, of the Associated Oil Company at Ventura, California.

Occurrence—Ventura, Locality 161.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 304, 305, Loc. 161.

Pinus masoni Dorf, new species
(Plate 5, figs. 4 to 6)

Portions of two flattened, carbonized cones found in the Pico shales and one complete carbonized cone from the Merced are referable to this species.

Description—Cones asymmetric with an uneven base; ovate in shape; 6 to 8 cm. long, 5 to 6 cm. wide; unopened; scales on the outer side 22 to 27 mm. long, 12 to 17 mm. wide at the apex, decreasing toward the base of the cone; umbos produced into rounded, asymmetrical knobs, decreasing in width, increasing in length and becoming more conical toward the base of the cone, and bearing evidence of having been terminated by prickles

pointing obliquely upward; scales on the inner side of cones small, poorly developed, quadrangular, and nearly flat; seeds not preserved.

Discussion—Among living species of which cone material was examined, the present species is closely related to the western closed-cone pines, more especially *Pinus muricata* D. Don. from which it is hardly distinguishable. The cones of *P. attenuata* Lemmon are clearly related but differ particularly in being more tightly closed and in the umbos' being more symmetrical, more angular, much less recurved and pointing almost directly outward rather than obliquely upward.

Among the very numerous fossil species of *Pinus*, the present species is most clearly related to *P. muricata* D. Don. of the Pleistocene tar pits at Rancho La Brea,¹ differing mainly in size and development. *P. attenuata* Lemmon of the Pliocene or Pleistocene Auriferous gravels² is clearly of the same general closed-cone type, as is also *P. knowltoni* Chaney of the Mascall Miocene of Oregon,³ a species which is also represented in the flora of the Payette Miocene of Eastern Oregon and adjacent Idaho,⁴ the Eagle Creek Oligocene along the Columbia River, Oregon,⁵ and the Bridge Creek Oligocene of the Crooked River, Oregon.⁶ Both Mason and Chaney refer *P. knowltoni* to the living *P. attenuata*, whose general relationship to *P. masoni* has already been intimated above.

The modern *Pinus muricata* is found only along the California coast from sea-level to about 1000 feet elevation from Fort Bragg on the north to the islands west of Los Angeles on the south. The occurrence of *P. masoni*, its Pliocene equivalent, in the marine sediments of the Merced and Pico formations directly on the present coastline suggests a similar habitat and climatic conditions comparable to those which exist along the coast today.

The species is named in honor of Mr. Herbert L. Mason of the University of California.

Occurrence—Ventura, Locality 161; Mussel Rock, Locality 159.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 306, 307, Loc. 161., Plesiotype, No. 308, Loc. 159.

Pinus sp.

(Plate 6, fig. 1)

The remains of this pine are represented by a carbonaceous impression of a highly weathered or rodent-gnawed cone, lacking sufficiently diagnostic characters to warrant a specific determination, but noteworthy as representing a type of pine hitherto unknown in the fossil state.

The impression itself is 21 cm. long and about 3 to 4 cm. wide, and is probably the remnant of a wider, if not also longer, cone of cylindrical shape. The projections extending outward from the core suggest an open cone. The size, shape and few details preserved in the specimen indicate a possible close relationship to the modern *Pinus lambertiana* Dougl.

The occurrence of our species in an interior lake deposit is particularly consistent with the present distribution of *Pinus lambertiana*, which is generally found at elevations of 1000 to 7000 feet from the Cascades in Oregon southward along the inner Coast Ranges and Sierra Nevada. The weath-

¹ Mason, Carnegie Inst. Wash. Pub. No. 346, pt. V, 147, pl. 3, figs. 1, 4, 5, 1927.

² Mason, op. cit., 148, pl. 2, fig. 2.

³ Mason, op. cit., 148, pl. 2, fig. 1, pl. 3, figs. 3, 6, 7.

⁴ Chaney, Amer. Jour. Sci., vol. 4, 214, 1922.

⁵ Chaney, Univ. Chicago, Walker Mus. Contr., vol. 2, No. 5, 160, pl. 5, figs. 3, 4, 1920.

⁶ Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 101, 1927.

ered condition of the cone, in a matrix which at the same locality has preserved much more delicate plant material, such as ferns, suggests that it was weathered by transportation, perhaps in a stream, from a somewhat higher elevation.

Pinus lambertiana is one of the dominants of the Sierra-Cascade Forest, occurring at the drier middle elevations of the California mountain slopes. It is significant to note that among its associates are *Libocedrus decurrens* Torr. and *Pseudotsuga taxifolia* Brit., both of which have their counterparts in the fossil associates of *Pinus* sp. Among the genera of shrubs of the same association, *Ceanothus*, *Quercus*, *Amelanchier*, *Cercocarpus*, *Prunus* and *Ribes* have their corresponding equivalents in the Santa Clara flora.

Occurrence—Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., No. 309, Loc. 160.

Genus PSEUDOTSUGA Carr.

Pseudotsuga sonomensis Dorf, new species

(Plate 6, figs. 2 to 4)

Impressions of cones, carbonized remnants of cones, and wood referable to this species have been found in five localities. The following description is based on the three best impressions of cones, two of which are counterparts, from the Sonoma tuffs.

Description—Cones ovate, open, 4 cm. long, 3 cm. wide; scales 12 mm. long, 10 mm. wide (estimated), thin, slightly concave, rounded at the apex, emerging obliquely from the central axis; bracts and seeds not preserved. Twigs and associated needles of the *Pseudotsuga* type, found in the same deposits, are probably of the same species. They appear to be two-ranked on the twig, 20 mm. long, narrow, and flat.

Discussion—Examination of cones and cross-sections of cones of the western *Pseudotsuga taxifolia* Brit. presents a striking similarity to both the impressions and the carbonized material found. The association of the species with *Sequoia langsdorfi* is similar to the modern association of *S. sempervirens* and *Pseudotsuga taxifolia* in the redwood border association of the California Coast Ranges.

The only cone species of *Pseudotsuga* reported from the Tertiary of North America are a series of carbonized cones from the Merced Pliocene¹ and a badly water-worn cone from the Santa Clara Pliocene² of central California, all of which are referred to the modern *P. taxifolia*. *Pseudotsuga* cone material from both these formations has been seen or collected by the writer. It undoubtedly represents the same species as described above, which is indistinguishable from the modern species.

The discovery of open cones of *Pseudotsuga* in the Sonoma formation is convincing evidence of the subaerial deposition of the volcanic ash making up the formation, as *Pseudotsuga* cones are known to close tightly in less than ten minutes when immersed in water. This paleobotanical criterion for the type of sedimentation is in perfect accord with the strong intimation of the petrographic examination of the ash for subaerial deposition.

Occurrence—Petritified Forest, Locality 150; Garberville, Locality 157; Santa Rosa, Locality 154; Mussel Rock, Locality 159; Calabazas Canyon, Locality 160.

¹Lawson, Univ. Calif. Dept. Geol., Bull., vol. 1, 146, 1893.

²Hannibal, Bull. Torr. Bot. Club, vol. 38, 335, 1911.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 310, 311, 312, Loc. 150; Plesiotype, No. 313, Loc. 150., No. 314, Loc. 154; No. 315, Loc. 157.

Family TAXODIACEÆ

Genus SEQUOIA Endl.

Sequoia langsdorfii (Brnt.) Heer

(Plate 6, figs. 5, 6)

S. langsdorfii (Brnt.) Heer, Fl. Tert. Helv., vol. 1, 54, pl. 20, fig. 2; pl. 21, fig. 4, 1855.

Fossil leaf impressions of this species in the Pliocene are indistinguishable from the modern coast redwood, *Sequoia sempervirens* Endl. In view of the lack of conclusive cone material in association with the leaves, the forms are here referred to the common Tertiary species, from which they are equally indistinguishable. Silicified wood occurring in the same deposits have been identified by Mrs. Irma E. Webber as indistinguishable from the modern coast redwood.

The Pliocene occurrence of *Sequoia* has already been pointed out by Mason,¹ who refers the leaves and wood to the modern species. The leaves of *Sequoia* during the Tertiary are so consistently alike that it becomes a matter of speculation as to where *S. langsdorfii* should be replaced by *S. sempervirens*. Inasmuch as all the heretofore described Tertiary forms have been referred to the former it appears incongruous to refer the Pliocene leaves to the modern species without more conclusive evidence.

The significance of *S. langsdorfii* in the Pliocene is rather in its rarity than its abundance when contrasted with the profusion of its leaves in the Miocene. In the 16 localities from which plant remains have been studied the species is common only in 2, scarce in 3, and entirely lacking in the remaining 11. This condition may indicate actual scarcity, a situation distant from the site of deposition or destruction during transportation. The absence of most of the more typical redwood associates and the preservation of much more delicate plant material in the same sediments strongly suggests adverse environmental conditions for more than a scattered or very localized distribution of the species, such as obtains today on the outer borders of the redwood forest proper. The association of *S. langsdorfii* with equivalents of the typical members of the less humid border forests also suggests that in contrast to the Miocene, the *Sequoia* forest was nowhere the dominant cover but that it continued throughout the Pliocene in the few scattered places where moisture conditions were favorable for limited groves of the redwood and its hardier associates.

Occurrence—Petrified Forest, Localities 150, 151; Bennett Valley, Locality 153; Garberville, Locality 157; Santa Rosa, Locality 154.

Collection—Univ. Calif. Coll. Pal. Bot., Plesiotype, No. 316, Loc. 151., Plesiotype, No. 317, Loc. 154; No. 318, Loc. 150; No. 319, Loc. 153; No. 320, Loc. 157.

¹ Mason, Carnegie Inst. Wash. Pub. No. 346, pt. V, 153, 1927.

Family CUPRESSACEÆ

Genus LIBOCEDRUS Endl.

Libocedrus sp.

(Plate 6, fig. 8)

Two small fragments referable to this genus have been collected from one locality. Each fragment consists of small scale-like decurrent leaves arranged in unlike opposite pairs, exactly as in the modern *Libocedrus decurrens* Torr., the only representative of this genus in western North America. The latter species is recorded in fossil from the Mascall Miocene¹ of Oregon, and is hard to separate from our species. In view of the scanty nature of the fragments and in the absence of seeds or cones it is thought best not to make a specific determination at this time.

This species is not common in the Pliocene of California. Perhaps, like its modern equivalent, it favored the intermediate mountain slopes, where its chances for fossilization were relatively small. Among its fossil associates, *Pseudotsuga sonomensis* and *Pinus* sp. suggest a similarity of the assemblage to the mixed upland association of the medium heights of the Sierra Nevada and inner Coast Ranges, where *Pinus lambertiana*, *Pseudotsuga taxifolia* and *Libocedrus decurrens* are commonly found together.

Occurrence—Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., Nos. 321, 322, Loc. 160.

CLASS ANGIOSPERMÆ

SUB-CLASS MONOCOTYLEDONES

ORDER LILIALES

Family SMILACACEÆ

Genus SMILAX Linné

Smilax sp.

(Plate 6, fig. 7)

The single incomplete specimen figured is the only representative of this genus encountered in the localities studied. Although enough of the leaf is preserved to make a definite generic determination, it is thought best not to describe it as a new species until better and more definite evidence is obtained.

It is difficult to correlate specifically the fragmentary specimen with other Tertiary forms, although its generic characters are of essentially the same type as shown in several figured specimens. It seems most closely related to *Smilax lamarensis* Knowlton from the Latah Miocene,² though differing considerably in the tertiary venation. *S. wardii* Lesquereux from the Mascall Miocene³ and *S. magna* Chaney from the Eagle Creek Oligocene⁴ are both much longer and more lanceolate in shape, with a distinctly different base.

Among the modern species of *Smilax*, the above species is quite similar to the western *S. californica* Gray. Sheet No. 2904 in the herbarium of

¹ Mason, Carnegie Inst. Wash. Pub. No. 346, pt. V, 155, pl. 5, figs. 3, 7, 9, 10, 11, 1927.

² Berry, U. S. Geol. Surv. Prof. Pap., 154-H, 240, pl. 63, fig. 15, 1929.

³ Lesquereux, U. S. Nat. Mus. Proc., vol. 11, 19, pl. 13, fig. 1, 1888.

⁴ Chaney, Univ. Chicago, Walker Mus. Contr., vol. 2, No. 5, 161, pl. 6, fig. 1, 1920.

The New York Botanical Garden contains leaves which are essentially the same in shape, size and venation as those observed in the Pliocene specimen.

The modern *Smilax californica* is rather limited in range, extending only from southern Oregon to Butte County, California. It is commonly associated with the mesophytic redwood elements but often extends into the redwood border forests along the stream banks. The association of the Pliocene species with *Sequoia langsdorfii*, *Pseudotsuga sonomensis* and a few broad-sclerophylls and chaparral species suggests a habitat similar to that of the more open redwood border forest rather than the redwood forest proper.

Occurrence—Petrified Forest, Locality 150.

Collection—Univ. Calif. Coll. Pal. Bot., No. 323, Loc. 150.

SUB-CLASS DICOTYLEDONES

ORDER SALICALES

Family SALICACEÆ

Genus POPULUS Linné

Populus alexanderi Dorf, new species

(Plate 6, figs. 9 to 11; plate 7, figs. 1 to 3)

This species is one of the dominants of the Pliocene flora, as is indicated in its occurrence at nine localities, in most of which it is represented by many well-preserved specimens.

Description—Leaves sub-coriaceous to thin; 5.5 to about 10 cm. long; 4 to 9 cm. broad at the middle; oval to lanceolate-ovate, truncate to slightly cordate at the base, contracted above to an obtusely, or in some cases acutely, acuminate apex; margin evenly crenate-serrate above a more or less entire base, the teeth unsymmetrical, acute and pointing upward; petiole rarely preserved, stout and up to 2.5 cm. in length; midrib straight, strong; 5 to 7 pairs of strong secondaries, opposite at the base to alternate toward the apex, in a few cases opposite again near the tip; secondaries diverging from the midrib at rather inconstant angles varying from 30° to 90°, the basal pair fairly straight in some cases, but usually curving upward toward the margin, becoming finer and either forking with terminations in the marginal teeth, or indistinctly joining the ones next above; basal secondaries usually giving off 3 to 6 tertiary branches from their abaxial sides at approximately 40° angles, the basal branches given off at or very near the intersection of the lowermost secondaries and the midrib; these basal tertiaries sub-parallel to each other, curving slightly upward and forking or joining the ones next above similarly to the larger secondaries; other tertiary veins very irregularly percurrent.

Discussion—This species is particularly abundant in the Pliocene localities studied and is sufficiently well preserved to be fairly diagnostic. It is quite variable in size, general shape and finer details of venation; such variations as are seen are equally characteristic of the leaves of the modern poplars of western North America. In some cases, indeed, the variable leaf forms of the living forms so closely approximate each other that the species can not be separated on leaves alone. This must be kept in mind in comparing the fossil forms with recent species, as it is likely that the Pliocene poplar may, in fact, contain a combination of certain characters which have subsequently become specific differences in two, three, or even more of the modern species.

All three of the common living poplars of the west, *Populus trichocarpa* Torr. and Gray, *P. tremuloides* Michx. and *P. fremontii* S. Wats., show a general similarity to the present species, but the closest resemblance is with *P. trichocarpa*, from which many of the specimens, especially those from the Santa Clara and Alturas localities, are almost indistinguishable. In general, the Pliocene form is more broadly ovate and less acuminate pointed than the modern equivalent, although lanceolate forms do occur along with the ovate forms at the two localities just mentioned.

A comparison with numerous herbarium sheets of *Populus trichocarpa* at The New York Botanical Garden and the Field Museum, Chicago, has shown that the variations noted in size, shape and venation in the fossil species are equally well shown in most of the sheets of the modern form. A number of herbarium sheets containing the modern *P. trichocarpa* from the herbarium of Leland Stanford Junior University, collected in the vicinity of the university, present the same variations with a slightly more open type of venation. A complete survey of all the sheets of this species in the herbarium of The New York Botanical Garden seems to indicate that the mature, full-grown leaves are characteristically larger and thinner in the northern, more humid sections of the Pacific Coast (especially the Cascade Mountains of western Washington, and Vancouver Island, B. C.), whereas the smaller, thicker ones typify the southern or drier portions, such as Southern California or western Nevada. A similar comparison can be made between the Pliocene specimens from the north and those from the south or interior.

The striking similarity of our species to the modern as well as the numerous Tertiary poplars makes the generic determination unquestionable. There are, however, numerous fossil species which have maintained exceedingly consistent leaf forms throughout the entire Tertiary, making it almost a matter of personal judgment as to whether or not the species described above may be a variable leaf type of a previously recorded form. The justification for making it a new species is based on the consistence of its more important characters in the abundant specimens from nine localities and its closer relationship to the modern form than to any figured Tertiary form in America.

Notable among its close relatives is the variable *Populus lindgreni* Knowlton, which is recorded from the Payette,¹ Mascall² and Latah³ Miocene floras of the northwest. The type specimens of *P. lindgreni* were compared with the present species at the U. S. National Museum and were found to differ mainly in their more orbicular shape, their symmetrical teeth and the stronger tendency of their secondaries to terminate in the marginal teeth. A fairly good comparison of the larger leaves, of which two are figured, is seen with *P. eotremuloides* Knowlton from the Payette Miocene.⁴ *Populus balsamoides* Göpp., of the Miocene Auriferous gravels⁵ and the Miocene of Yellowstone Park⁶ and *P. pyrifolia* Kirchner of the Florissant Miocene⁷ are of the same general type. Among the European

¹ Knowlton, U. S. Geol. Surv., 18th Ann. Rpt., pt. 3, 725, pl. 100, fig. 3, 1898.

² Knowlton, U. S. Geol. Surv., Bull. 204, 29, pl. 2, fig. 1, 1902.

³ Knowlton, U. S. Geol. Surv. Prof. Pap. 140, 31, pl. 14, figs. 4-7, 1926.

⁴ Knowlton, U. S. Geol. Surv., 18th Ann. Rpt., pt. 3, 725, pl. 100, figs. 1, 2; pl. 101, figs. 1, 2, 1898.

⁵ Lesquereux, U. S. Geol. Surv. Terr., vol. 8, 248, pl. 55, figs. 3-5, 1883.

⁶ Knowlton, U. S. Geol. Surv. Mon. 32, pt. 2, 696, pl. 86, fig. 1, 1899.

⁷ Kirchner, St. Louis Acad. Sci., Trans., vol. 8, 185, pl. 15, fig. 4, 1898.

forms several species bear a rather marked resemblance, notably *P. emarginata* Göpp¹ and *P. eximia* var. *producta* Göpp.,² though to a lesser degree than the American Tertiary forms.

Populus trichocarpa is widely distributed along river bottoms and canyons from Alaska southward along the Coast Ranges and Sierra Nevada to southern California, in most cases at altitudes of 3000 to 6000 feet, although it does occur as low as 500 feet. *Populus alexanderi* is found with species suggestive of a similar stream-bank association, comparable to that of the southern coast ranges where a growth of *Platanus*, *Alnus*, *Pseudotsuga*, *Salix*, *Quercus*, *Populus* and occasional redwoods and associates make up a rather open type of forest growth.

This species is named in honor of Miss Annie M. Alexander.

Occurrence—Garberville, Localities 155, 156; Alturas, Locality 165; Santa Rosa, Locality 154; Bennett Valley, Locality 152; St. Mary's College, Locality 162; Lafayette Dam, Locality 163; Calabazas Canyon, Locality 160; Coalinga, Locality 164.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes Nos. 324, 325, Loc. 152; Cotype, No. 326, Loc. 155; Cotype, No. 327, Loc., 156; Plesiotypes, Nos. 328, 329, Loc. 165; Plesiotype, No. 330, Loc. 162; Plesiotype, No. 331, Loc. 163.

***Populus prefrementii* Dorf, new species**

(Plate 7, fig. 4)

Six specimens of this species have been obtained from four localities. They are sufficiently well preserved to justify a specific determination, as they all present characters which indicate that they are distinct from *Populus alexanderi* described above.

Description—Leaves broadly deltoid to reniform, invariably wider than long, narrowing to an acutely acuminate or slightly rounded apex, and very abruptly to a wide, truncate or slightly cordate base; length from 4 to 5 cm.; width from 5 to 6.2 cm.; petiole not preserved; midrib thin, but firm and straight; 6 to 9 pairs of thin, opposite to alternate secondaries, diverging from the midrib at an obtuse angle approaching 90° near the base and somewhat less toward the apex; secondaries curving widely upward, becoming obscured near the margin; tertiary venation indistinct; margin coarsely serrate, the teeth large, rounded, and asymmetrically pointing toward the apex; texture sub-coriaceous, as indicated by the indistinct venation and the curling of the borders in a few of the specimens.

Discussion—This species is clearly distinguished from *Populus alexanderi* by its greater width in comparison to its length and by its larger, coarser and more rounded serrations. In these distinguishing characters it immediately suggests *P. fremontii* S. Wats. of the interior valleys of California. It has, indeed, been impossible to separate many of the herbarium leaves of this modern species from the Pliocene form, as is suggested in the name of the latter.

Among the numerous Tertiary species of *Populus* very few have been observed whose leaf characteristics are comparable to those of *P. prefrementii*. The figure of *P. latior* Al. Br., from the Eocene of Alaska³ and the Oligocene of British Columbia⁴ indicates that this species is somewhat

¹Göppert, Tert. Fl. von. Schosnitz, 24, pl. 15, figs. 2-4.

²Op. cit., pl. 16, figs. 3, 4.

³Heer, Fl. Foss. Alaska, 25, pl. II, fig. 4, 1869.

⁴Penhallow, Rept. Tert. Pl. Brit. Col., 77, 1908.

similar in shape and marginal characters, and is certainly of the same general type, even if not specifically equivalent.

The living *P. fremontii* is characteristic of the southern Coast Ranges and interior valleys of central and southern California, where it is common with willows, sycamore, alder and ash along living streams. In the northern Coast Ranges it is rare and confined to the inner valleys. The associations and distribution of its Pliocene relative suggests similar conditions of growth and a wider distribution, including the coastal portion of the central Coast Ranges, where it is absent in the modern flora.

Occurrence—Bennett Valley, Locality 152; Lakeville, Locality 158; St. Mary's College, Locality 162; Lafayette Dam, Locality 163.

Collection—Univ. Calif. Coll. Pal. Bot., Cotype, No. 332, Loc. 162.

Genus *SALIX* Linné

Salix coalingensis Dorf, new species

(Plate 7, figs. 5 to 7; plate 8, figs. 1, 2)

Remains of this species are particularly abundant in the Pliocene deposits of California, being present at nine localities. Only one other species, *Populus alexanderi*, is as widely distributed. The following description is based on three of the best-preserved specimens from Coalinga and one from St. Mary's College.

Description—Leaves rather firm in texture, narrowly lanceolate, 3.5 to 11.4 cm. long, 1.2 to 2.6 cm. wide, broadest at about the middle, then tapering gradually to a cuneate base and an acutely, or rarely, obtusely acuminate apex; margin usually entire, sometimes finely serrate; petiole stout and apparently short; midrib strong for the size of the blade; secondaries 10 to 18 pairs, thin, mainly alternate, arising from the midrib at an obtuse or nearly right angle, then curving upward usually rather abruptly and running for a considerable distance near the margin, ultimately joining the ones next above; finer venation forming a close network of irregularly quadrangular areas, often obscure.

Discussion—All specimens examined are characteristically *Salix* in all details. To attempt a close correlation with any living species is no easy matter, due to the degree of variability exhibited in the leaves of modern willows, most of which can not be identified by modern botanists on leaf characters alone. A complete survey of all available American willows was made at The New York Botanical Garden, and a careful examination of the western willows was made at the Field Museum, Chicago, and at the University of California. There is a rather close resemblance of the species to several of the California willows, notably *Salix lasiolepis* Benth., *S. laevigata* Bebb., *S. lasiandra* Benth. and *S. sitchensis* Sanson, all of which present the same kind of variations in size, shape and marginal characters as does *S. coalingensis*. On the average, however, *S. laevigata* is consistently serrate-margined and more obtuse at the base; *S. lasiandra* is usually serrate-margined and more acutely tapered at the apex; and *S. sitchensis* is more commonly broader and more obtusely pointed at the base and apex than the fossil species. *S. lasiolepis*, with its tendency toward an entire margin and its variations in size and shape coinciding with those observed in the fossil, is perhaps the closest modern correlative. Several herbarium sheets, chiefly Nos. 4927, 7717 and 1446 at The New York Botanical Garden, and No. 7164 at the Field Museum exhibit the same variations as are noted in the fossil specimens.

There are several previously described Tertiary willows which show the same tendencies as *Salix coalingensis*. *S. californica* Lesquereux from the Crooked River Oligocene¹ and the Miocene Auriferous gravels,² the types of which were studied at the U. S. National Museum, is of the same entire-margined type as most of the specimens of our species, but differs chiefly in a more acute apex, more obtuse base and a more open type of venation. A general relationship, however, is strengthened by Chaney's comparison of *S. californica* to the same modern species, *S. lasiolepis*, mentioned in the foregoing discussion of our species. *S. remotidens* Knowlton from the Latah Miocene³ is rather similar in venation and marginal characters, differing mainly in a more obtuse base and a more acute tip. The larger specimens of our species agree closely with *S. elongata* from the Miocene of Elko, Nevada⁴ and Yellowstone Park Miocene,⁵ though the latter is more lanceolate in shape. *S. libbeyi* Lesquereux from the Florissant Miocene,⁶ *S. angusta* Al. Braun., a widely distributed Tertiary species,⁷ and *S. vaccinifolia* Knowlton of the Esmeralda Miocene⁸ show tendencies which resemble somewhat those observed in some of the Pliocene specimens. Among the European willows, *S. wyomingensis* Kn. and Cockerell (formerly *S. integra* Göpp.), from the Swiss Tertiary⁹ seems very closely related, especially to the smaller forms from the Wildcat. None of the Tertiary forms studied seems close enough, in the opinion of the writer, to make possible a specific correlation.

The modern western willows mentioned above as possible correlatives of *Salix coalingensis* are typical stream-border species of the Coast Ranges and Sierra Nevada foothills of California. The association of *S. lasiolepis*, which is the most common willow throughout the lower elevations of California, with sycamore, poplar and alder, and the association of *S. lasiandra* with alders, poplars and sycamore, and *S. laevigata* with alders, poplars and other willows, suggests the same ecological conditions of growth for the Pliocene willow, which is nearly always found with sycamore and poplars, and usually also with alder, ash, chinquapin and live-oaks, indicative of a stream-bank habitat in a region supporting mainly an open type of forest growth.

Occurrence—Garberville, Localities 155, 156; Alturas, Locality 165; Santa Rosa, Locality 154; Lakeville, Locality 158; St. Mary's College, Locality 162; Lafayette Dam, Locality 163; Calabazas Canyon, Locality 160; Coalinga, Locality 164.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 333, 334, 335, Loc. 164; Cotype, No. 336, Loc. 162; Plesiotypes, Nos. 337, 338, Loc. 155.

Salix sp.

(Plate 8, fig. 3)

Several good specimens of a willow distinctly different from *Salix coalingensis* above have been collected at three localities. Other material of this same type has been seen and studied in the collections of Stanford

¹ Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 103, pl. 8, figs. 8-11, 1927.

² Lesquereux, Mus. Comp. Zool., Mem. vol. 6, No. 2, 10, pl. 1, figs. 18-20, 1878.

³ Knowlton, U. S. Geol. Surv. Prof. Pap. 140, 32, pl. 12, fig. 7, 1926.

⁴ Lesquereux, U. S. Geol. Surv. Terr., vol. 7, 169, pl. 22, figs. 6, 7, 1878.

⁵ Knowlton, U. S. Geol. Surv., Mon. 32, pt. 2, 698, 1899.

⁶ Lesquereux, U. S. Geol. Surv. Terr., vol. 8, 156, pl. 31, fig. 3, 1883.

⁷ Lesquereux, U. S. Geol. Surv. Terr., vol. 7, 168, pl. 22, fig. 5 only, 1878.

⁸ Knowlton, U. S. Geol. Surv., 21st Ann. Rpt., pt. 2, 212 pl. 30, figs. 8, 20, 1901.

⁹ Heer, Tert. Fl. Schweiz, vol. 2, 32, pl. 68, figs. 20-22, 1856.

University. Unfortunately, none of the specimens is complete enough to make a full description possible.

The leaves of this willow are very narrow, long and lanceolate, with entire or remotely serrate margins; the narrow width is rather consistent for the entire length of the blade; the base and tip have not been observed; the midrib is strong and straight, the secondaries fine, numerous and arching upward along the margin.

Among living willows it seems clearly related to *Salix exigua* Nuttall,¹ a widely distributed willow which ranges from British Columbia south through the Pacific ranges to southern California. Hannibal has previously referred similar material from the Santa Clara beds² to *Salix fluviatilis*. On the basis of leaves alone, particularly in so uniform a type as the willow group, it seems more reasonable to relegate the fossil leaf material to a new species, which would have been completely described and named at this time were it not for the lack of better specimens.

Salix exigua occurs chiefly along lowland streams, ponds and lakes, often mingled with poplars and other stream-border types. These same types are the common associates of the Pliocene species.

Occurrence—St. Mary's College, Locality 162; Lafayette Dam, Locality 163; Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., No. 339, Loc. 162.

ORDER FAGALES

Family BETULACEÆ

Genus ALNUS Gaertner

Alnus merriami Dorf, new species

(Plate 8, figs. 6, 7)

The description of this new species is based entirely on the numerous well-preserved specimens from the Wildcat formation along the Eel River. Specimens collected from the Merced sandstone, the Sonoma tuffs and the Santa Clara beds can not be separated from the Wildcat leaves and are therefore referred to the same species.

Description—Leaves broadly ovate to ovoid, narrowing gradually to a bluntly cuneate base and an obtusely acuminate tip, sometimes rather abruptly; length from 3.5 to 10 cm. (estimated), width from 2.5 to 7 cm. (figured specimen, pl. 8, fig. 6 is below the average size); petiole not preserved; midrib stout, straight or sometimes curving slightly near the base and tip; 9 to 12 pairs of prominent secondaries, opposite to sub-opposite, or in a few cases becoming alternate in the upper half of the leaf, diverging from the midrib at a 50° to 60° angle, straight, or in some cases curving slightly outward from the midrib and recurving slightly upward toward the margin, all terminating in the marginal teeth; middle secondaries giving off 1 to 3 strong tertiary branches from their abaxial sides always at distances more than halfway out from the midrib (usually much more); these tertiaries curving obtusely outward and terminating in the smaller teeth; other tertiaries regularly percurrent, closely set and at right angles to the secondaries; margin doubly serrate, the coarse, blunt teeth at the ends of the secondaries being the more prominent, while the finer serrations which terminate the tertiaries on the lower portions of the large

¹ Formerly designated as *Salix fluviatilis exigua* (Nutt.) Sargent.

² Hannibal, Torrey Bot. Club., Bull. 38, 336, 1911.

teeth are less conspicuous and more finely pointed; all teeth point slightly upward toward the apex of the leaf; texture rather firm.

Discussion—A comparison with living representatives of this family makes the generic reference rather certain. Finer comparisons within the genus bring out a closer relationship to the western alders than to any other North American species. It is by no means a simple matter to separate the three modern alders of the West, *Alnus rubra* Bong., *A. tenuifolia* Nutt. and *A. rhombifolia* Nutt., on leaf characters alone. From a study of numerous herbarium sheets of the three species, the closest relationship of our leaves seems to be with *A. rhombifolia*, although many leaves of the latter seem to tend toward a less broadly ovate shape, to have more acute and straighter secondaries and to be less conspicuously doubly serrate, as most of the teeth are of about the same small size, finely pointed and directed outward rather than upward. Some of the specimens collected, however, are indistinguishable from *A. rhombifolia* and might easily be referred to it without further hesitation were it not for the fact that all gradations are present from these to the larger, less rhombifolia-like types, and that it is equally difficult to separate leaves of any of the living western alders from one another.

Contrasting the normal tendencies of *A. rubra* and *A. tenuifolia*, the latter seems to be rounded, with a more cordate base and a doubly serrate margin in which the secondary teeth are very prominent, sharply pointed and directed outward, and are present on the upper as well as the lower portions of the primary teeth. *A. rubra*, on the other hand, is more ovate, with a more cuneate base and a doubly serrate margin in which the secondary teeth are quite inconspicuous, point upward and are not present on the upper portions of the primary teeth. It will thus be seen that the venation, shape and margin characters of our species tend more toward the average *A. rhombifolia* or *A. rubra* type than toward *A. tenuifolia*.

In spite of certain normal, average tendencies in the modern leaves it was noted, with regret, that in many of the herbarium sheets which were studied, especially in those of *Alnus rubra* and *A. rhombifolia*, similarities in leaf form occurred which made it absolutely impossible to designate any one set of characters as being positively uniform in any one species. Perhaps it is reasonable to assume that the differentiation into the three closely related living species had not, at least noticeably, taken place in the Pliocene.

There is, however, one constant tendency in the distribution of the modern alders which is noticeable in their Pliocene ancestors: *Alnus rubra* is distinctly a more northern and *A. rhombifolia* a southern type. This condition is apparent among the Pliocene leaves, the northern forms of which seem to resemble the normal *A. rubra* type while the southern forms come closer to *A. rhombifolia*. It would perhaps have seemed more logical to distinguish two species in the Pliocene were it not for the overlapping of variations and the difficulty of defining the modern species on the basis of leaves alone.

Among the species of *Alnus* described from the Tertiary there are a number which show a relationship, though not sufficiently close to warrant specific identity. The figured specimens of *A. corralina* Lesq. from the Miocene Auriferous gravels¹ as well as the types studied at the National

¹ Lesquereux, U. S. Geol. Surv. Terr., vol. 8, 243, pl. 51, figs. 1-3, 1883.

Museum bear a striking resemblance, differing mainly in having more rounded bases, more prominent secondary teeth and tertiary branches extending more than halfway down the secondaries. A new species of alder, *A. prerhombifolia* Berry from the Latah Miocene,¹ of which the type specimens were examined, shows a general similarity, though differing notably in shape, venation and margin. It is also possible that *Alnus* sp. Chaney from the Mascall Miocene may be similar or identical to our species as Chaney describes it² as being doubly serrate and mentions *A. rubra* as a closely related form. *A. kefersteini* (Göpp.) Unger, from the Alaskan Miocene³ differs mainly in a more cordate base and less distinct serrations of equal size. *A. carpinoides* Lesquereux from the Bridge Creek Oligocene⁴ is much less prominently doubly serrate, with the secondary teeth of the same or approximately the same size as the primary ones, and with the secondaries diverging from the midrib at a more acute angle.

The living *Alnus rubra* is found from Alaska to central California, especially along the outer coast ranges. It is a member of the redwood forest proper, but it is somewhat tolerant of the less humid conditions of the redwood border forest, where it may be found along streams at lower altitudes in association with willows, poplars, Douglas firs, maples and others. *A. rhombifolia* ranges from Idaho and southeastern Oregon along the great valley to southern California, living along the banks of streams mingled with sycamores, ashes, poplars, willows, live-oaks, dogwoods and chaparral species. It is thus seen that the ecological conditions for the growth of each of these alders may not be very different, though on the average *A. rubra* favors more mesophytic situations than *A. rhombifolia*. The consistent association of *Alnus merriami* with willows, poplars, sycamores, ashes, chinquapins, oaks and chaparral types, and its absence at localities where the more mesophytic redwood elements are dominant suggests an ecological equivalence to *A. rhombifolia*.

The species is named in honor of Dr. John C. Merriam, President of the Carnegie Institution of Washington.

Occurrence—Garberville, Localities 155, 156; Bennett Valley, Locality 152; Lakeville, Locality 158; Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot. Cotypes, 340, 341, 342, Loc. 156; Plesiotype, No. 343, Loc. 160.

Family FAGACEÆ

Genus QUERCUS Linné

Quercus lakevillensis Dorf, new species

(Plate 8, figs. 4, 5)

Several good specimens of this species have been collected at four of the localities in California. The description which follows is based on four well-preserved specimens, two of which are figured, from the Merced sandstone and the Sonoma tuffs.

Description—Leaves ovate, elliptical to oblong, narrowing abruptly to a rounded or cordate base and to an acutely, or sometimes obtusely, acuminate tip; length from 2.2 to 4 cm.; width from 1.7 to 2.4 cm.; petiole not

¹ Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 244, pl. 50, fig. 11, 1929.

² Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 26, 40, 1925.

³ Heer, Fl. Foss. Arct., vol. 2, abt. 2, 29, pl. 3, figs. 7, 8, 1869.

⁴ Lesquereux, U. S. Geol. Surv. Terr., vol. 8, 243, pl. 50, fig. 11; pl. 51, figs. 4, 4a, 5, 1883.

preserved; midrib stout near the base, gradually becoming slender toward the apex; 4 to 6 pairs of slender secondaries, sub-opposite to alternate, sub-parallel to irregularly spreading, the angle of divergence from the midrib varying from almost 90° near the base to as low as 35° toward the apex; secondaries more widely spaced along the midrib toward the apex, where they tend to branch at about half their length, the branches, as well as the lower secondaries, terminating in the marginal teeth; finer venation quite indistinct, forming an irregular network; margin rarely entire, usually 3 to 6 pairs of lobate teeth, attenuate or only slightly produced into short spines; texture coriaceous as indicated by the convexity of the leaf and the faint preservation of the finer venation.

Discussion—Among the living oaks *Quercus lakevillensis* is clearly related to the evergreen oaks of western North America, especially to *Q. agrifolia* Née, the Coast Live Oak of California, from which it is impossible to separate the species on leaf characters alone. *Q. agrifolia* exhibits the same variations in venation, margin and shape as its Pliocene equivalent.

No other species of *Quercus* has been described from the Tertiary of America which is specifically comparable to our species, although several have been figured and described which show a close relationship to the group of evergreen western oaks. *Q. agrifolia* Née has been reported from the Pleistocene tar pits of Rancho La Brea.¹ Obviously, the relationship between these forms, which were seen by the writer at the University of California, and our Pliocene species is just as close or closer than that between the Pliocene and the modern form. There is, indeed, considerable doubt as to whether the Pliocene form should not be relegated to the modern species, the only objection being the lack of more confirmatory evidence, such as seeds and wood. Hannibal has reported *Q. agrifolia* as occurring rarely in the Pliocene Santa Clara beds.² Chaney's tentative revision of the Santa Clara flora³ also includes a species of oak which he correlates with the modern *Q. agrifolia*. An examination of Hannibal's types at Leland Stanford Junior University and a study of the writer's oak material from the same locality has brought out a much closer similarity of the toothed leaves to the spinose-toothed varieties of *Q. chrysolepis* Liebm. In view of the abundance of entire leaves of the *Q. chrysolepis* type in the same beds it is reasonable to suppose that a number of its toothed varieties should also be found, as happens at the St. Mary's College locality. Hence the toothed forms from the Santa Clara beds are referred to *Quercus hannibali*, the Pliocene counterpart of *Q. chrysolepis* (see page 86).

It is possible that the Miocene species, *Q. convexa* Lesq.,⁴ may represent the fore-runner of the modern evergreen oaks; in leaf details it resembles more closely the evergreen *Q. engelmannii* Greene and *Q. wislizenii* A. DC. than it does *Q. agrifolia*, indicating rather a general than a specific relationship to our species. The same group resemblance is shown in *Q. clarnensis* Trelease from the Crooked River Oligocene,⁵ though its similarity to the *Q. agrifolia* type is much less striking than to *Q. chrysolepis* or *Q. tomentella* Engelm. The evidence, in so far as the fossil records show, seems to

¹ Frost, Univ. Cal. Pub., Dept. Bot., vol. 14, No. 3, 81, pl. 15, figs. 5-9, 1927.

² Hannibal, Torrey Bot. Club, Bull. 38, 335, 337, 1911.

³ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 45, 1925.

⁴ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 39, 40, 1925.

⁵ Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. 4, 111, pl. 10, figs. 10-13; pl. 11, figs. 1-7, 9, 10, 1927.

indicate that the evergreen oaks have only recently, perhaps only since the beginning of the Pliocene, become split into the various species now recognized. The characters of *Quercus lakevillensis*, representing the *Q. agrifolia* type, have certainly not been encountered in the Tertiary record of the west before the Pliocene.

The living *Quercus agrifolia* is found today on the dry mountain slopes and canyon sides of the California Coast Ranges. It is a common constituent of the more open type of the broad-sclerophyll forest, overlapping in the northern Coast ranges into the redwood border forest. A similar habitat seems to have obtained for its Pliocene relative, which is consistently found together with redwood border or more xerophytic types in all four of the California localities.

Occurrence—Lakeville, Locality 158; Bennett Valley, Locality 153; Petrified Forest, Localities 150, 151.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 344, 345, Loc. 158; Cotype, No. 346, Loc. 153; Cotype, No. 347, Loc. 151.

Quercus bockéi Dorf, new species

(Plate 9, figs. 1 to 3)

This species is one of the dominants in the lower horizon of the Sonoma tuff flora, but is absent at all other localities, even within the tuffs themselves. Over 300 specimens have been examined, making possible a very complete and comprehensive study of the species. Were it not for the abundance of material presenting all gradations in size, shape and specific details, it is quite possible that two or more species would have been recognized.

Description—Leaves obovate to obovate-lanceolate, narrowing gradually to a slightly asymmetrical cuneate base and abruptly to an acuminate to elongate-acuminate or caudate-acuminate tip; length from 5 to 16 cm.; width from 1.5 to 5.5 cm.; average dimensions 4.5 by 13.5 cm. (see plate 9 fig. 1); petiole stout, 0.5 to 1.8 cm. long, rarely well preserved; midrib heavy, straight or slightly curved below the middle; 12 to 15 pairs of secondaries, sub-opposite to alternate, mostly the latter, sub-parallel, diverging from the midrib at an angle of 50° to 60°, slightly less basally and more apically, straight or more commonly curving slightly upward and terminating in the marginal teeth except in the basal portion where the teeth are only poorly if at all developed; in a few instances the secondaries fork near the middle, each branch ending in a marginal tooth; tertiary venation distinct, coarse, and irregularly percurrent at approximately right angles to the secondaries, except in the central portion of the blade where the veins arch in and connect with the midrib; margin dentate except near the base, the teeth bluntly-tipped, equilateral and pointing outward or only slightly upward; texture coriaceous.

Discussion—A study of modern genera with leaves of this type indicates that the foliar distinctions between *Quercus*, *Fagus* and *Castanea* are in most cases very difficult to make. *Fagus* leaves are generally more ovate, more sharply dentate with the teeth pointing upward, and the secondaries curving outward rather than upward. In *Castanea* the shape is only rarely obovate, more generally ovate, with the marginal teeth more prominent and usually produced into long spinose points curving upward toward the apex of the leaf. The tip is, to be sure, sometimes elongate as in a few of the fossil specimens. Among the modern species of *Quercus* many were

found which agree much more closely than any of the species of *Castanea* or *Fagus* which were examined. Particularly was this true of a group of Mexican and Central American oaks¹ including *Quercus oocarpa* Liebm., *Q. cyclobalanoides* Trelease, *Q. reevesii* Trelease and *Q. galeottii* Martens. Comparisons made at The New York Botanical Garden indicate a closer resemblance to *Q. galeottii* Martens² than to any other species seen. This species now grows in the warmer zones of the Eastern Sierra Madre region of Mexico (Santiago de Huatusco, at 800 to 1800 meters).

Among living forms of American oaks *Quercus bockéei* shows a fair comparison with the eastern chestnut-oaks, such as *Q. muhlenbergii* Engelm., though the leaves of the latter have more lobate margins with larger teeth. In western America *Q. sadleriana* R. Br. Campst. and *Q. (Lithocarpus) densiflora* (H. and A.) Rehd. are of somewhat the same type. *Q. sadleriana* leaves tend toward a cuneate base, as in the species above, have identical venation, but more prominent teeth on the larger forms; *Q. (Lithocarpus) densiflora* have a more rounded or even cordate base, much more obtuse secondaries, but marginal teeth of the same character.

There are several fossil species from the Tertiary of North America which have the general appearance of *Q. bockéei*. *Q. nevadensis* Lesquereux from the Miocene Auriferous gravels³ suggests a close relationship, differing chiefly in being wider with less regularly spaced, straighter secondaries with a stronger tendency toward forking and curving up near the margin, sending a finer tertiary into the teeth and in having much less prominent serrations. As only two specimens of *Q. nevadensis* are known, it is possible that the recovery of a larger number would bring out an even closer relationship or identity. *Q. schofieldii* Hollick from the St. Eugene silts of late Tertiary age⁴ is represented by only one specimen which is larger and wider, with smaller unequilateral marginal teeth, a larger number of secondaries and finer tertiary venation. It is clearly of the same general type, however, as is indicated by Hollick's comparison with the same Mexican oaks and with *Q. nevadensis*. *Q. consimilis* Newberry, which is recorded from the Mascall Miocene⁵ and the Bridge Creek and Crooked River Oligocene⁶ is generally less obovate and narrower with more irregular secondaries and larger, unequal marginal teeth. Chaney considers⁶ *Q. (Lithocarpus) densiflora* as its "closely related modern species," which, aside from its foliar similarity, suggests a relationship to *Q. bockéei*. *Q. horniana* Lesquereux from the Mascall Miocene⁷ is much less obovate with large, prominent, sharply pointed marginal teeth. *Q. clarnensis* Trelease from the Payette Miocene⁸ and the Bridge Creek Oligocene,⁹ as well as the figures of its various synonyms enumerated by Chaney, is usually much smaller, more acutely pointed and with a more rounded base and teeth more prominent, as in *Q. horniana* mentioned above. Other Tertiary forms which bear some resemblance to *Q. bockéei*, but more remotely than those

¹ Trelease, *American Oaks*, Nat. Acad. Sci., vol. 20, 45, 1924.

² Hollick figures a drawing of this species in Mem. N. Y. Bot. Garden, vol. 7, pl. 44, fig. 3, 1927.

³ Lesquereux, Mus. Comp. Zool., vol. 6, No. 2, 5, pl. 2, figs. 3, 4, 1878.

⁴ Hollick, Mem. N. Y. Bot. Garden, vol. 7, No. 4, 403, 427, pl. 33, 1927.

⁵ Newberry, U. S. Geol. Surv., Mon. 35, 71, pl. 43, figs. 2-5, 1898.

⁶ Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 112, 1927.

⁷ Knowlton, U. S. Geol. Surv. Bull. 204, 52, pl. 8, fig. 1, 1902.

⁸ Chaney, Amer. Jour. Sci., vol. 4, 216, 1922.

⁹ Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 111, pl. 10, figs. 10-13; pl. 11, figs. 1-7, 9, 10, 1927.

already considered, include *Q. idahoensis* Knowlton from the Payette Miocene,¹ *Q. gaudini* Lesquereux from the Puget Eocene² of Washington, and *Q. grönlandica* Heer from the Kenai Eocene³ of Alaska.

It is interesting to note how the oaks of the *Q. bockéi* type have become less and less numerous during the course of the Tertiary, until today only a few survivors remain in the Pacific states, the majority having been relegated to a much more southerly habitat. The presence of so many leaves of this species in but one of the sixteen localities, and their closer relationship to Miocene and modern Mexican, rather than Californian, types suggests a lower Pliocene or even upper Miocene age for the beds involved. The flora, scanty as it is, is not typically Miocene, in which case *Q. bockéi* must be regarded as a Miocene relict type, making its last stand against the rigors of a region being subjected to a gradual cooling and drying accompanied by continual volcanic outbursts which destroyed the forest growth, thus reducing the possibilities for the reappearance of the species which were not in adjustment with the changing environmental conditions. Its absence at the other Pliocene localities may be attributed to the fact that the sediments at the Petrified Forest localities are the only ones in which upland types were preserved.

Finally, it must be pointed out that in spite of the similarity of *Q. bockéi* to previously described oaks and modern oaks, there remains the possibility of finding additional material which will corroborate the generic reference or change it definitely to *Castanea* or *Fagus*, or perhaps to *Lithocarpus*. Some such evidence has already been presented in a report on silicified wood from the same locality,⁴ which indicates the presence of two species of oak, a pine, an elm and a redwood, but no chestnut or beech. If the generic reference of *Q. bockéi* is correct, the presence of two leaf species of oaks in the flora (see *Q. lakevillensis* above) would be in perfect agreement with the wood determinations. If it is *Castanea* or *Fagus* we must account not only for the absence of one leaf species of oak but also for the absence of *Castanea* or *Fagus* wood. The combined evidence presented seems to favor the reference to *Quercus*.

The association of *Q. bockéi* with several redwood border forest species suggests that in the modern forest it finds its ecological equivalent in *Q. (Lithocarpus) densiflora*, which is characteristic of the mixed forest of the interior mountains and of the redwood border forest, as well as the redwood forest proper of the Coast Ranges of California.

This species is named in honor of Mrs. D. G. Bockée, present owner of "The Petrified Forest."

Occurrence—Petrified Forest, Locality 150.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 348, 349, 350, 351 Locality 150.

Quercus hannibali Dorf, new species

(Plate 8, figs. 8 to 11)

Leaves of this species are abundant at each of the two localities where it is present. It is possible that at least two distinct species might have been recognized among the specimens collected were it not for the presence

¹ Knowlton, U. S. Geol. Surv., 18th Ann. Rpt., pt. 3, 729, pl. 102, fig. 4, 1898.

² Lesquereux, U. S. Nat. Mus. Proc., vol. 10, 39, pl. 2, figs. 7, 8, 1887.

³ Heer, Fl. Foss. Arct., vol. 1, 108, pl. 8, fig. 8; pl. 10, figs. 3, 4; pl. 11 fig. 4; pl. 47, fig. 1, 1868.

⁴ Platen, Natur-Forschenden Gesellschaft zu Leipzig, vol. 34, 4-26, 1907.

of gradational forms and the close comparison of all variations to those present in the closely related living species, *Quercus chrysolepis* Liebm.

Description—Leaves usually ovate to orbicular at the one extreme and slightly obovate at the other, narrowing rather abruptly, or in some cases gradually, to a rounded or slightly cuneate base; tip varying from abruptly acuminate or cuspidate to elongate acuminate; length from 1 to 4.4 cm; maximum width from 0.8 to 1.9 cm., average dimensions of the most common type (entire, ovate; see plate 8, fig. 9) 1.3 by 2.9 cm.; petiole short and stout, 2 or 3 mm. long; midrib stout; 5 to 12 pairs of prominent, parallel to sub-parallel secondaries, sub-opposite to alternate, diverging from the midrib at an angle of 60° to 80° (in a few instances as high as 90°), terminating in the marginal teeth or, in the entire-margined forms, turning abruptly upward near the border; tertiary venation indistinct; margin commonly entire though sometimes partly to completely dentate or sinuate-dentate, the teeth usually sharply pointed outward; texture coriaceous. There are several obscure impressions of acorn cups which may be referable to this species.

Discussion—The leaves of *Quercus hannibali* have been compared with all the available herbarium material of western North American oaks. Several of the live-oaks, especially *Q. chrysolepis* Liebm., *Q. tomentella* Engelm., and *Q. agrifolia* Née, are quite similar in average leaf form. The entire-margined variants of *Q. tomentella* are essentially the same in most characters but the dentate forms present a type of tooth quite distinct from any observed in the fossil specimens. Although rather similar in shape and texture, the leaves of *Q. agrifolia* are distinctly different in venation and marginal characters (see page 83). It is decidedly difficult, on the other hand, to separate the fossil forms from any of the leaf forms of *Q. chrysolepis*. As in the modern form, the average leaf of the fossil species is entire, ovate and essentially parallel-veined. The dentate varieties present the same type of teeth as observed in the living form. Minor variations in size, shape and details of venation are equally well shown in both the living and fossil material. In spite of this very close approximation it is thought best to refer the fossil forms to a distinct new species in view of the lack of more convincing evidence.

The few obscure acorn-cup impressions which may be referable to the same species are not unlike those of *Q. chrysolepis* var. *hansenii* Jepson of Amador County, California. In general, the acorn cups of the modern *Q. chrysolepis* are distinctly larger than those observed in the Santa Clara deposits.

Among related fossil species it must be noted that the description of this new species is based partly on material from the Santa Clara beds in Calabazas Canyon, from which Hannibal had previously collected similar leaves, which he referred to the living *Quercus chrysolepis*.¹ In view of the lack of more confirmatory evidence and of the similarity in leaf form of several western live-oaks, it is thought best to refer the fossil leaves to a new species, stating, however, that among the living oaks it resembles the leaves of several of the live-oak group, more especially *Q. chrysolepis*.

Quercus hannibali is apparently rather closely related to *Q. transgressus* Lesquereux from the Miocene Auriferous Gravels.² The absence of any figure of this species and the failure of the writer to find the type specimen

¹ Hannibal, Torrey Bot. Club, Bull. 38, 337, pl. 5, figs. 2, 9, 1911.

² Lesquereux, Mus. Comp. Zool., Mem. vol. 6, No. 2, 59, 1878.

at the U. S. National Museum makes this relationship uncertain. The short description published indicates at least the same general type of leaf. *Quercus* n. sp. from the Payette Miocene,¹ also unfigured; must also be of the same type, as it is referred to as "strikingly like the western *Q. chrysolepis*." *Q. convexa* Lesquereux from the Miocene Auriferous gravels² and the Mascall Miocene resembles in a general way the entire leaves of several of the western evergreen live-oaks, as has already been pointed out by Chaney.³ It tends, however, to be more lanceolate in shape, with more numerous secondaries, and is not known to be dentate. No earlier Tertiary forms are comparable, suggesting that this live-oak type did not begin to be well defined until late in the Tertiary.

The evergreen type of oaks is abundant today in exposed situations along the Pacific Coast. *Quercus chrysolepis* favors the ridges, open slopes and valley sides of the inner Coast Ranges and the Sierra Nevada, where it is one of the dominants of the scattered broad-sclerophyll forest formation.⁴ There is every indication in the mingling of *Q. hannibali* with xerophytic or semi-xerophytic associates at both localities that it occupied similar situations during the Pliocene, even so far as to be confined to localities within the outer Coast Ranges.

This species is named in honor of Dr. Harold Hannibal, formerly of Leland Stanford Junior University.

Occurrence—Calabazas Canyon, Locality 160; St. Mary's College, Locality 162.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 352, 353, Loc. 160; Cotypes, Nos. 354, 355, 356, Loc. 162.

Quercus declinata Dorf, new species

(Plate 8, figs. 12, 13)

About ten good specimens of this species have been collected, mostly from the Santa Rosa locality, in which it is the dominant leaf type. It is easily separated from the other Pliocene oaks and is very consistent in most of its diagnostic features.

Description—Leaves ovate to ovate-lanceolate, narrowing abruptly to an obtusely cuneate or slightly cordate base, the tip rather obtusely acuminate; length from 3.6 to 6.9 cm.; width from 1.8 to 2.8 cm.; average dimensions 2.5 by 4.5 cm. (see plate 8, fig. 12); petiole apparently short and stout, rarely well preserved; midrib strong, straight to slightly curved; 8 to 12 pairs of strong secondaries, sub-opposite to alternate, diverging from the midrib at an angle as high as 90° near the base to 50° or 60° near the apex, and always terminating in the marginal teeth; tertiary venation distinct in a few specimens, forming an irregular network between the basal secondaries to a more regular, percurrent system near the apex; margin regularly dentate, the teeth large, bluntly tipped and pointing upward and slightly outward; texture coriaceous, as evidenced by the curled condition of several specimens.

Discussion—In leaf details *Quercus declinata* is not like any of the more common oaks of California. It is distinctly of the type of *Q. tomentella*

¹ Chaney, Amer. Jour. Sci., vol. 4, 219, 1922.

² Lesquereux, Mus. Comp. Zool., Mem. vol. 6, No. 2, 4, pl. 1, figs. 13-17, 1878.

³ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 39, 1925.

⁴ Cooper, *The Broad-sclerophyll Vegetation of California*, Carnegie Inst. Wash. Pub. No. 319, 21, 1922.

Engelm., an evergreen oak found only on the islands off the coast of southern California, where it grows on exposed slopes and more open situations along streams and canyon bottoms.

This species of oak, like several other of the Pliocene oaks, is of the evergreen type which has not often been encountered in the earlier Tertiary deposits of America. The general characters, especially of the teeth and venation, suggest *Quercus boweniana* Lesquereux from the Miocene Auriferous gravels,¹ though the latter differs considerably in shape and a more acutely acuminate base. *Q. peritula* Cockerell from the Miocene Florissant beds² is of the same type, though differing in venation and character of the marginal teeth. Some of the smaller leaves of *Q. clarnensis* Trelease from the Crooked River Oligocene³ are much like the few more lanceolate specimens of our species. *Q. crossii* Knowlton from the Denver Eocene⁴ is also suggestive of the same general type. The figured specimens of *Rhus boweniana* Lesquereux⁵ and *R. dispersa* Lesquereux⁶ from the Miocene Auriferous gravels are rather suggestive of *Quercus* of the evergreen type. They are essentially of the same character as the leaves of *Quercus declinata* and should probably be referred to as least the same genus.

The association of *Q. declinata* with species including poplar, willow, alder, chinquapin, live-oaks and an occasional redwood and fir suggests conditions not unlike the open forests in which the modern *Q. tomentella* is found.

Occurrence—Santa Rosa, Locality 154; Bennett Valley, Locality 152.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 357, 358, Loc. 154; Cotype, No. 359, Loc. 152.

***Quercus orindensis* Dorf, new species**

(Plate 9, figs. 6 to 9)

Leaf impressions of this species are particularly abundant in the Orinda formation at the St. Mary's College locality, and are found also, but in a more fragmentary condition, at three other localities. The following description is based entirely on the more complete specimens from the St. Mary's College locality.

Description—Leaves obovate to obovate-lanceolate or lanceolate, narrowing gradually to an acutely acuminate base and more abruptly to an acute, pointed, sometimes prolonged apex; length from 3.5 to 6.5 cm; maximum width from 1.5 to 2.9 cm.; petiole rather thin and up to 9 mm. long; midrib rather stout, usually straight or but slightly curved; 6 to 10 pairs of slender secondaries, sub-opposite to irregularly alternate, leaving the midrib at an angle of 30° to 50° or rarely as high as 80°, and terminating either in the marginal teeth or the sinuses between the teeth; finer venation indistinct; margin with 3 or 4 pairs of lobate teeth, though in some cases the lobate character is not pronounced; teeth sharp-pointed and directed slightly upward; texture rather firm or sub-coriaceous as indicated by the curling of the leaves and the indistinct tertiary venation.

Discussion—Among the modern species of western oaks studied in the herbarium of the University of California it was found difficult to separate

¹ Lesquereux, Mus. Comp. Zool., Mem., vol. 6, No. 2, 6, pl. 2, figs. 5, 6, 1878.

² Cockerell, Am. Mus. Nat. Hist., Bull. 24, 85, 1908. (Figured as *Quercus mediterranea* Unger in Lesquereux, U. S. Geol. Surv. Terr., vol. 8, pl. 28, fig. 9, 1883.)

³ Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 111, pl. 10, figs. 11, 13, 1927.

⁴ Knowlton, U. S. Nat. Mus., Proc., vol. 10, 39, pl. 2, figs. 5, 6, 1887.

⁵ Lesquereux, Mus. Comp. Zool. Mem., vol. 6, No. 2, 29, pl. 9, figs. 8, 9, 1878.

⁶ Lesquereux, op. cit., 32, pl. 1, fig. 23.

the leaves of *Quercus orindensis* from those of *Q. douglasii* Hook. and Arn. The same variations in size, shape and marginal characters are present in both species; the modern species seems to tend toward a slightly more obtuse and rounded apex, although it is acute and pointed in some cases as in the fossil form. Sheet No. 5571, collected in Amador County, presents leaves of the same size, shape and marginal characters, as well as several with an acute apex as in the fossil; sheet No. 5570, also from Amador County at 2000 feet, contains many leaves of the same lobate character as well as several in which the lobes are not well pronounced, as in a few of the fossil specimens (see plate 9, fig. 8).

Quercus orindensis bears considerable resemblance to a group of closely related species from the Latah Miocene, including *Q. merriami* Knowlton,¹ a form much larger than our species and with more regular secondaries and more numerous teeth; *Q. payettensis* Knowlton,² also larger and with more numerous teeth; and *Q. rustii* Knowlton,³ which is likewise larger, but more similar than the former two in marginal and venation characters. *Q. merriami* is also found in the Mascall Miocene⁴ and *Q. payettensis* in the Payette Miocene.⁵ In his recent revision of the Latah flora, Berry⁶ suggests that all the species mentioned above are probably variants of the dominant *Quercus cognatus* Knowlton, a much larger and more lobate form, in which case the leaves of *Q. orindensis* are not so closely related, since they are normally much smaller and with fewer and less prominent lobes than the normal leaf of the Latah species.

Quercus douglasii is characteristic of the dry foothills and inner Coast Ranges of California, where it may form pure stands or may be associated with *Pinus sabiniana* and *Quercus wislizenii*. It is one of the most xerophytic of the California oaks, occurring as one of the first chaparral species above the dry grasslands, and but rarely associated with the elements of the broad-sclerophyll forest. The fossil associates of *Q. orindensis* suggest a somewhat similar habitat of dry, open slopes bordering stream valleys by the presence of several chaparral species, a few elements of the broad-sclerophyll forest, several riparian species and an occasional redwood and fir.

Occurrence—Santa Rosa, Locality 154; St. Mary's College, Locality 162; Lafayette Dam, Locality 163; Coalinga, Locality 164.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 360, 361, 362, Loc. 162; Plesiotype, No. 363, Loc. 154.

Genus CASTANOPSIS Spach.

Castanopsis chrysophylloides Lesquereux

(Plate 9, figs. 4, 5)

Castanopsis chrysophylloides Lesquereux, Mus. Comp. Zool., Mem. vol. 6, No. 2, 9, pl. 2, fig. 10, 1878.

Leaves of this species have been collected at three localities, though they are not abundant at any. They are characteristically lanceolate or

¹ Knowlton, U. S. Geol. Surv., Prof. Pap. 140, 35, pl. 19, figs. 4, 5, 1926.

² Knowlton, op. cit., 37, pl. 21, figs. 5-7.

³ Knowlton, op. cit., 26, pl. 21, figs. 3, 4.

⁴ Knowlton, U. S. Geol. Surv. Bull. 204, 49, pl. 6, figs. 6, 7; pl. 7, figs. 4, 5, 1902.

⁵ Knowlton, U. S. Geol. Surv., 18th Ann. Rpt., pt. 3, 730, pl. 102, fig. 9, 1898.

⁶ Berry, U. S. Geol. Surv., Prof. Pap. 154-H, 245, 246, 1929.

oblong-lanceolate in shape, gradually narrowing to an acuminate base and apex, the latter rather contracted into a fine point. The margin is entire and slightly undulate and the secondaries are obtuse, approaching an angle of divergence of 90° and looping upward abruptly near the margin; texture is coriaceous.

The Pliocene specimens are as indistinguishable from the modern *Castanopsis chrysophylla* A. DC. as they are from Lesquereux's species, to which they are referred above. An even closer comparison is seen with the smaller leaved *C. chrysophylla* var. *minor* Benth. The figure of *C. chrysophylloides* from the Miocene Auriferous gravels¹ is larger and broader and with slightly more acute secondaries—slight variations which are equally well shown in the leaves of the modern form. *C. chrysophylloides* is also recorded from the Mascall Miocene.² No other representatives of this genus have been reported from the Tertiary of North America. Several other genera, however, contain species which seem rather closely related to our form. *Quercus simulata* Knowlton from the Payette Miocene³ and the Latah Miocene,⁴ the type specimens of which were consulted at the U. S. National Museum, is of the same general form, differing chiefly in size, more acute venation and a tendency toward being sparsely toothed. *Q. elena* Ung. from the Florissant Miocene⁵ and some of the figured specimens of *Q. elenoides* Lesquereux from the Miocene Auriferous gravels⁶ are also of the same type. *Umbellularia dayana* (Kn.) Berry from the Latah Miocene⁷ is scarcely distinguishable in general characters, as is also *Sapindus affinis* Newberry from the Eocene of Yellowstone Park.⁸ It is apparent, as Chaney has already pointed out,⁹ that a revision of the several species of the *Castanopsis chrysophylla* type is necessary before a better understanding of the Tertiary history and distribution of the genus can be obtained.

The modern *Castanopsis chrysophylla* is a characteristic member of the broad-sclerophyll forest of California. The association of its Pliocene equivalent with broad-sclerophyll, redwood, riparian and occasional chaparral elements suggests somewhat similar requirements of growth. The scarcity of the leaves of *C. chrysophylloides* in the Pliocene sediments may be due to the widespread restriction during this epoch of the Redwood element, with which the modern species is most commonly associated.

Occurrence—Santa Rosa, Locality 154; Lakeville, Locality 158; Bennett Valley, Locality 152.

Collection—Univ. Calif. Coll. Pal. Bot., Plesiotype No. 364, Loc. 154; Plesiotype No. 365, Loc. 152.

¹ Lesquereux, Mus. Comp. Zool., Mem., vol. 6, No. 2, 9, pl. 2, fig. 10, 1878.

² Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 26, 31, 36, 1925.

³ Knowlton, U. S. Geol. Surv., 18th Ann. Rpt., pt. 3, 723, pl. 102, figs. 1, 2, 1898.

⁴ Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 246, pl. 51, figs. 6, 7, 9-11, 1929.

⁵ Lesquereux, U. S. Geol. Surv. Terr., vol. 8, 155, pl. 28, figs. 11, 13, 1883.

⁶ Lesquereux, Mus. Comp. Zool., Mem. vol. 6, No. 2, 4, pl. 1, figs. 10 and 11 only, 1878.

⁷ Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 260, pl. 58, fig. 4, 1929.

⁸ Knowlton, U. S. Geol. Surv., Mon. 32, pt. 2, 736, pl. 102, figs. 1-3, 1899.

⁹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 26, 1925.

ORDER URTICALES

Family ULMACEÆ

Genus ULMUS Linné

Ulmus brownellii Lesquereux

(Plate 10, figs. 1, 2, 3, 10)

Ulmus brownellii Lesquereux, U. S. Geol. Surv. Terr., vol. 8, 160, pl. 28, figs. 2, 4, 1883.

Only four specimens of this species have been found at a single locality. These represent the only record of the genus *Ulmus* in the Pliocene deposits of California. None of the specimens is perfect, but enough of the details are preserved to enable a recognition of the typical *Ulmus brownellii* characteristics. The leaves are small, the largest being only 4 cm. long; they are distinctly asymmetrical at the base, slender-tipped and simple-serrate margined. No other species of *Ulmus* from the Tertiary of North America presents the same combination of features, notably the small size and simple serrate margin. *U. brownellii* is found in the Florissant Miocene¹ and the Crooked River Oligocene,² where it is associated with forms which indicate a rather open forest comparable to the slopes and ridges of the redwood border forest of California.

Ulmus brownellii is apparently present in the Pliocene flora as a relict species from the Miocene. A study of the genus in the Tertiary record of the west indicates that it has become less and less a common element of the floras from the Eocene through the Pliocene, finally resulting in its complete absence from the Pleistocene and modern floras west of the Rockies. Whether this has been due to adverse environmental conditions or to competition with hardier forms, or other causes, can not be ascertained, but it is significant to note that the Pliocene form is not of the normal, more mesophytic type of elm but is rather of a more xerophytic type, comparable to the small-leaved form of the modern *Ulmus parvifolia* Jacq., which thrives as a possible relict species under adverse conditions in northern China and Japan. Such may have been the case with *U. brownellii* during the Pliocene, since its association with riparian and chaparral species of semi-arid aspect seems hardly consistent with the mesophytic habitat in which the modern species of *Ulmus* seem best to thrive. In spite of the xerophytic aspect of the leaves of *U. brownellii*, the species does not seem to have been able to compete with the hardier elements of the Pliocene and hence did not survive to the present. The successful cultivation of *Ulmus americana* as a shade tree on the streets of Berkeley, California, might seem to suggest that the absence of native elms from the modern flora were due more to competition than to adverse environmental conditions. It must be remembered, however, that the early years in the lives of such cultivated trees are spent in nurseries, where they are carefully guarded against any adverse conditions which would otherwise prevent the tree from properly thriving.

Occurrence—Lafayette Dam, Locality 163.

Collection—Univ. Calif. Coll. Pal. Bot., Plesiotypes, Nos. 366, 367, 368, 369, Loc. 163.

¹ Lesquereux, U. S. Geol. Surv. Terr., vol. 8, 160, pl. 28, figs. 2, 4, 1883.

² Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 113, pl. 12, figs. 3, 6, 7, 8; pl. 13, figs. 1, 3, 4, 6, 1927.

ORDER RANALES

Family BERBERIDACEÆ

Genus ODOSTEMON Rafinesque

Odostemon hollicki Dorf, new species

(Plate 10, figs. 7, 8)

This species is known from only one locality, where it is represented by two specimens, one of the upper portion of a leaf, the other of the lower portion of another, or possibly the same leaf. The specimens are not complete but are well preserved and show sufficiently well that the species is distinct from any previously described or figured, in view of which the species is here named and described as completely as possible.

Description—Leaves broadly ovate to orbicular, narrowing gradually to an obtuse, rounded apex; base not preserved, probably truncate or slightly cordate; length about 7 cm.; width 6 to 7 cm.; midrib stout and straight; 6 to 8 pairs of prominent secondaries, subopposite at the base to alternate at the apex, leaving the midrib at an angle of 40° to 60°, straight for about two-thirds their length, then turning abruptly upward and forming a series of wide loops with the one next above; in one case a basal secondary branches conspicuously, each branch looping upward as in the other secondaries; tertiaries prominent, forming irregular quadrangular areas between the secondaries; margin spinose-dentate, the teeth widely spaced, pointing slightly upward and terminating the prominent tertiaries outside the looped secondaries; texture somewhat coriaceous, as indicated by the undulate margin and curled tip.

Discussion—Among the living western species of *Odostemon*, all of which are referred to the genus *Berberis* by Jepson¹ and to *Mahonia* at The New York Botanical Garden, the present species is most similar to *Odostemon aquifolium* Pursh., whose leaves were closely compared and found to be of the same size, texture, margin and venation, though the teeth are a little more closely spaced than in *O. hollicki*. Most of the species of *Odostemon* in the west are smaller, with larger, spiny and more attenuate teeth, comparable to the Tertiary *O. simplex* (Newb.) Cockerell.² Only one other western form, *O. nervosus* Rydb., is at all comparable to our species, though it is not as similar in details as *O. aquifolium*.

Only two species of *Odostemon* are recorded from the Tertiary of America: *O. simplex* from the Crooked River Oligocene,² the Bridge Creek Oligocene³ and the Payette Miocene,⁴ and *O. florissantensis* Cockerell from the Florissant Miocene.⁵ Both species differ considerably from *O. hollicki*, being distinctly ovate with sharply lobate margins, the teeth few and produced into long spines. The closely related genus, *Berberis*, is only represented by one questionable Tertiary form, *Berberis* (?) *gigantea* Knowlton,⁶ a large, tri-lobed, spiny leaf of a very different character.

Both *Odostemon aquifolium* and *O. nervosus* are widely distributed in the coniferous forests of the Coast Ranges and Sierra Nevada, extending north as far as British Columbia. The association of *O. hollicki* with

¹ Jepson, *Manual of the Flowering Plants of California*, 393, 1925.

² Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 116, pl. 14, figs. 7, 8, 9, 11, 1927.

³ Newberry, U. S. Geol. Surv., Mon. 35, 97, pl. 56, fig. 2 (figured and described as *Berberis*), 1898.

⁴ Chaney, Amer. Jour. Sci., vol. 4, 216, 1922.

⁵ Cockerell, Amer. Mus. Nat. Hist. Bull., vol. 24, 91, 1908.

⁶ Knowlton, U. S. Geol. Surv. Bull. 204, 57, pl. 11, fig. 1, 1902.

Sequoia and *Pseudotsuga* is consistent with the occurrence of the modern species with the redwood and Douglas fir, whereas the absence of typical redwood associates in the fossil flora is correlative with the fact that the modern forms are more typically present in the exposed, open forests of the redwood border than in the redwood forest proper.

This species is named in honor of Dr. Arthur Hollick of The New York Botanical Garden.

Occurrence—Petrified Forest, Locality 150.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 370, 371, Loc. 150.

Family LAURACEÆ

Genus UMBELLULARIA Nutt.

Umbellularia oregonensis Chaney

(Plate 10, fig. 5)

Umbellularia oregonensis Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. IV, 59-62, pl. 1, figs. 1, 3, 5, 7, 1925.

A number of leaves, which are provisionally referred to the above species, have been collected at four Pliocene localities. They are clearly *Umbellularia* and might have been referred to a new species if more complete material had been collected. It is possible that the Pliocene form may be more closely related to the Miocene species, *Umbellularia* sp. Chaney, which occurs widely in the Mascall.¹ The lack of figured specimens, other than the few of *Salix pseudo-argentea* Knowlton² and *S. dayana* Knowlton,³ which Chaney thinks are referable to *Umbellularia*, makes a comparison rather difficult.

The specimens of our Pliocene species resemble the modern *Umbellularia californica* Nutt. as strikingly as do the figured specimens of *U. oregonensis* from the Oligocene. The living species is a characteristic member of the broad-sclerophyll forest of the California Coast Ranges, where it is often associated with typical redwood elements. Its Pliocene equivalent is found associated with abundant *Sequoia* leaves, but the absence of most of the typical redwood associates at this locality suggests a preservation of species of the more open type of the redwood border forest rather than the redwood forest proper. The total absence of *Umbellularia oregonensis* at 12 of the 16 localities is significant as evidence of the restriction of the more mesophytic forests during the Pliocene in California.

Occurrence—Petrified Forest, Localities 150, 151; Garberville, Locality 155; Lakeville, Locality 158.

Collections—Univ. Calif. Coll. Pal. Bot., Plesiotype, No. 372, Loc. 151; No. 373, Loc. 150; No. 374, Loc. 151.

ORDER ROSALES

Family PLATANACEÆ

Genus PLATANUS Linné

Platanus paucidentata Dorf, new species

(Plate 10, figs. 4, 9; plate 11, fig. 1; plate 12, fig. 1)

A large number of well-preserved specimens of this species have been collected at eight localities, in most of which it is one of the dominant

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 27, 36, 1925.

² Knowlton, U. S. Geol. Surv. Bull. 204, 31, pl. 2, figs. 2-4, 1902.

³ Knowlton, op. cit., 31, pl. 2, figs. 9, 10.

species. Though only a few of the specimens are whole, the abundance of material has made possible a rather complete description.

Description—Leaves highly variable in shape, primarily 5-lobed with the basal lobes appreciably smaller than the others; occasionally 3-lobed; lobes varying in shape from rather short and broad with shallow, obtuse sinuses to long and slender with deep, more acute sinuses; tips of lobes rounded or occasionally acuminate; base truncate, cuneate, or less commonly cordate-decurrent on the petiole; length 7.5 to 15.2 cm.; width from 8.2 to 17.8 cm.; average dimensions apparently about 9.5 by 11 cm.; petiole stout, up to 2.1 cm. long; the 5 primaries stout and straight, or slightly curved to flexuous, the central and two laterals branching from the top of the petiole while the basals are joined to the laterals at a short distance from, or occasionally very close to, the midrib; all primaries terminating in the tips of the lobes; 6 to 8 pairs of strong, alternate to subopposite secondaries present on the central primary, diverging at an angle of about 45° near the base and approaching 60° or 70° toward the tip, curving upward and forming a series of well-defined quadrangular loops with the ones next above; 3 to 5 pairs of secondaries of the same character present in the upper two-thirds of the lateral primaries; basal primaries supporting 4 to 5 unpaired secondaries of similar nature on their lower sides, there being usually only one or two present on their upper sides near their terminal extremities; tertiaries prominent, usually forming irregular, rectangular areas between the secondaries, or curved quadrangular areas between the lower portions of the secondaries and the primaries; occasional tertiaries present between and parallel to the secondaries; finer nervilles indistinct; margin nearly always entire and slightly revolute, though occasionally remotely dentate, the teeth small, blunt and pointing upward; when teeth are present they rarely terminate the secondaries but rather the small tertiaries arising from the lower surfaces of the marginal loops; texture coriaceous, as indicated by the curling of the lobes and the margin and by the indistinct venation on the impressions of the upper surfaces.

Discussion—Leaves of this character might easily be referred, on general appearance, to either *Acer* or *Platanus*. In view of this possibility the writer has carefully examined herbarium species of *Acer* as well as *Platanus* in the various herbaria, resulting in a very definite reference to the latter genus. The leaves of *Acer macrophyllum* Pursh., which are more like our form than any other American species of *Acer*, present consistently the following differences: primary lobes more obovate with well-defined large, marginal teeth, almost amounting to subsidiary lateral lobes, which always terminate the secondaries; these secondaries straighter, never arching upward or looping with the ones next above; base usually cordate; basal primaries nearly always branching off from the petiole at the same point as the central and lateral primaries; tertiary venation much less regular or distinct; texture usually much thinner. Such differences, added to the striking similarities of the specimens to *Platanus*, seem to make their reference to the latter genus unquestionable.

Of the three living species of *Platanus* in America, our species is clearly more closely related to the western *P. racemosa* Nutt. The tendency toward entirety is particularly a common feature of the two species in question, as contrasted to the serrate-margined eastern *P. occidentalis* L. Almost all of the leaves examined showed the same tendencies in shape, margin, base and venation as *P. paucidentata*, with perhaps a slight inclination toward being broader.

The widespread occurrence of *P. paucidentata* in the Pliocene helps to complete the interesting story of the genus in western America and is of particular significance in the study of the environmental conditions during that epoch. The living *P. racemosa* is confined to the stream-bottoms of the more arid Sierra foothills, inner Coast Ranges and southern outer Coast Ranges of California, where it is commonly associated with willows, poplars, alders, ashes, maples, walnuts and others. The Pliocene relative, *P. paucidentata*, was of somewhat similar habitat since willows, poplars, alders and ashes are among its commonest associates. During the Miocene, however, the species of *Platanus* seems to have occupied slightly more mesophytic habitats, correlative with the modern oak-madrone forest, as is suggested by its association with *Sequoia*, *Umbellularia*, *Arbutus*, *Acer* and the broad-leaved *Quercus pseudolyrata*.¹ During the Oligocene, two species of *Platanus* are similarly associated with redwood-border species, though the presence of typical redwood forest types such as *Sequoia*, *Torreya*, *Myrica*, *Corylus*, *Rhamnus* and *Cornus* suggests perhaps even more mesophytic conditions of growth.² Throughout this entire sequence, therefore, there seems to have been a progression in the species of *Platanus* from earlier, more mesophytic to later, more xerophytic habitats, culminating in the modern *P. racemosa*, which has been relegated to a semi-arid environment totally different from that of its living eastern relative, which has maintained its foothold in the mesophytic habitats east of the Rockies.

This same progression is also suggested in a study of the leaf characters of *Platanus* in the consecutive Tertiary horizons. From the Eocene to the present there has been a progressive trend from serrate-margined leaves of the mesophytic *P. occidentalis* type to entire-margined leaves of the xerophytic *P. racemosa* type.

No Tertiary species of *Platanus* appears to be closely related to *P. paucidentata*, in spite of the presence of over 15 species in the fossil record. A suggestion of a relationship is noted in *P. dissecta* Lesq. from the Miocene Auriferous gravels,³ which shows the same tendencies in shape variations, lobation and primary venation, but which is consistently and conspicuously serrate, as are most of the Tertiary sycamores. *P. condoni* (Newb.) Knowlton from the Bridge Creek Oligocene⁴ has a tendency toward entire margins, though it differs considerably from our species in size, shape and venation. Its status as a distinct species, moreover, is questioned by Chaney, who tentatively considers it to represent merely an aberrant phase of *P. aspera* Newb.⁵

Occurrence—Garberville, Localities 155, 156; Santa Rosa, Locality 154; Bennett Valley, Locality 152; Lakeville, Locality 158; St. Mary's College, Locality 162; Lafayette Dam, Locality 163; Coalinga, Locality 164.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 375, 376, Loc. 156; Cotypes, Nos. 377, 378, 379, Loc. 152; Cotypes, Nos. 380, 381, Loc. 164.

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 34-41, 1925.

² Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. I, 15-18, 1925.

³ Lesquereux, Mus. Comp. Zool. Mem., vol. 6, No. 2, 13, pl. 7, fig. 12; pl. 10, figs. 4, 5, 1878.

⁴ Newberry, U. S. Geol. Surv. Mon. 35, 85, pl. 56, fig. 1; pl. 58, fig. 1, 1898 (described and figured as *Ficus? condoni* Newb.).

⁵ Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 120, 1927.

Family GROSSULARIACEÆ

Genus RIBES Linné

Ribes stanfordianum Dorf, new species

(Plate 10, fig. 6)

A considerable number of specimens of this species has been collected at the Calabazas Canyon locality. Many, however, were evidently wrinkled and torn during the course of deposition so that only a few complete leaves were obtained. The single specimen figured, showing most of the characteristic details, was the most perfect leaf encountered.

Description—Leaves 3-lobed, or in a few cases with two supplementary basal lobes, the lobes short and broad, separated by shallow, open sinuses; base cordate; length 2 to 4 cm.; width 3 to 5 cm.; petiole rather thin and up to 1.7 cm. long; central primary and lateral pair of primaries thin, though well pronounced, branching from the top of the petiole and terminating in the principal lobes; most prominent secondaries are the basal pair, which are given off at or very close to the intersection of the primaries and sometimes terminate in a pair of subordinate lobes; the remaining secondaries straight, thin and diverging from the primaries and basal secondaries at an angle of 30° to 45° and terminating in the marginal crenations; those from the central primary are in 4 to 6 opposite, unbranched pairs, not counting the more prominent basal pair, and are straight or slightly curved upward and usually unbranched, though forking in a few cases; those from the lower side of the prominent basal secondaries are 2 to 4 in number, unbranched and unpaired; tertiary venation obscure; margin coarsely, unevenly crenate; texture rather thin, as indicated especially by the numerous wrinkled and torn specimens.

Discussion—This genus is very common in the modern flora of the west, 26 species having been described by Jepson from California alone. These he divides into two distinct subgenera, *Ribesia*, the currants, and *Grossularia*, the gooseberries.¹ From a careful survey of the herbarium material at The New York Botanical Garden it was evident that the distinction between the leaves of the different species was often difficult to make, but there was a decided tendency in the leaves of *Ribes stanfordianum* to be of the *Ribesia* type, resembling most closely *Ribes nevadense* Kell. and *R. viscosissimum* Pursh.

Among the few Tertiary representatives of this genus, *Ribes stanfordianum* is not unlike *R. protomelænum* Cockerell from the Florissant Miocene² and *R. fernquisti* Berry from the Latah Miocene.³ Neither of these, however, seems specifically equivalent to our species since they differ considerably in size, texture, base and details of venation. A study of specimens collected from the same Pliocene locality was made recently at Stanford University. It was evident that the leaves which were doubtfully referred by Hannibal⁴ to *Grossularia menziesii* (Pursh.) Cov. and Brit. are the same as those which the writer has here referred to *Ribes stanfordianum*.

Ribes nevadense and *R. viscosissimum* are both found at comparatively high altitudes in the Sierra Nevada and Coast Ranges of California. Their resemblance to the fossil species suggests a similar habitat for the Pliocene

¹ Jepson, *Manual of the Flowering Plants of California*, 467, 1925.

² Cockerell, *Am. Mus. Nat. Hist. Bull.*, vol. 24, 92, pl. 7, fig. 15, 1908.

³ Berry, *U. S. Geol. Surv., Prof. Pap.* 154-H, 251, pl. 63, fig. 21, 1929.

⁴ Hannibal, *Bull. Torrey Bot. Club*, vol. 38, 337, 1911.

form. This suggestion becomes more significant when corroborated by the montane aspect of many of the fossil associates of *R. stanfordianum*, more particularly *Libocedrus* sp., *Pinus* sp. and *Ceanothus chaneyi*, whose modern correlatives, *Libocedrus decurrens*, *Pinus lambertiana* and *Ceanothus integerrimus* are characteristically found at higher altitudes.

This species is named for Leland Stanford Junior University, where the Santa Clara collections have been examined through the courtesy of the Department of Geology.

Occurrence—Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 382, 383, 384, Loc. 160.

Family ROSACEÆ

Genus CERCOCARPUS H. B. K.

Cercocarpus cuneatus Dorf, new species

(Plate 12, fig. 3)

This species is represented by two good specimens from one locality. The figured specimen is the more perfect, showing clearly most of the essential characteristics of the leaf form.

Description—Leaves ovate to slightly obovate, gradually narrowing to an obtusely rounded apex and a narrowly cuneate base; length 1.5 to 2.2 cm.; width 1 to 1.4 cm.; petiole not preserved; midrib straight; 4 to 6 pairs of opposite, parallel, unbranched secondaries, diverging from the midrib at an angle of 30° to 40° near the base to about 20° or 25° near the apex and terminating in the marginal serrations; tertiaries indistinct; margin entire along the basal half of the leaf where it parallels the lowest secondaries, and apparently simply serrate above the middle, although minor serrations may be obscured in the preservation; texture sub-coriaceous.

Discussion—Among the numerous species examined in various herbaria there are several western forms whose leaves closely resemble the Pliocene species. Six species are recorded by Jepson¹ from California, of which *Cercocarpus betuloides* Nutt. (formerly *C. parvifolius* var. *betuloides* Sarg.²) seems most closely related to our specimens.

Among fossil species it is apparent that this species was encountered by Hannibal in his collections from the same locality. He refers his specimens to the modern *C. betulæfolius* Nutt.,³ which is evidently the same as Jepson's *C. betuloides* Nutt. The practise of referring Tertiary forms to modern species on leaves alone has already been adversely commented upon (see p. 67), in view of which it seems more advisable to refer his specimens to the species just described. Only two other Tertiary species have been recorded: *C. antiquus* Lesquereux from the Miocene Auriferous gravels⁴ and the Mascall Miocene,⁵ and *C. orestesi* Knowlton from the Raton Eocene.⁶ Both of these are distinctly larger, more lanceolate and more obovate in average shape.

The living *Cercocarpus betuloides* is common on dry slopes and hillsides in the middle altitudes of the mountains west of the Rockies from Oregon to southern California. In California it is one of the shrubs in the

¹ Jepson, *Manual of the Flowering Plants of California*, 502, 1925.

² Sargent, U. S. Dept. Agric., Misc. Circ., No. 92, 154, 1927.

³ Hannibal, Bull. Torrey Bot. Club, 337, 1911.

⁴ Lesquereux, Mus. Comp. Zool. Mem., vol. 6, No. 2, pl. 10, figs. 6-11, 1878.

⁵ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 30, 33, 36, 1925.

⁶ Knowlton, U. S. Geol. Surv. Prof. Pap. 101, 325, pl. 95, fig. 2, 1918.

xerophytic chaparral association, suggesting a semi-arid habitat for its Pliocene counterpart. This suggestion seems well corroborated by the presence of several other chaparral species in the flora from Calabazas Canyon.

Occurrence—Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 385, 386, Loc. 160.

Genus PRUNUS B. & H.

Prunus merriami Knowlton

Prunus ? merriami Knowlton, U. S. Geol. Surv., Bull. 204, 67, pl. 11, figs. 2, 3, 6, 7, 1902.

Six incomplete though rather well-preserved specimens from three localities are provisionally referred to this species. The leaves are apparently ovate, with a rounded base and a finely serrate margin, the secondaries are obtuse and numerous, and the texture is coriaceous. All of these characteristics are present in the Mascall specimens as originally described by Knowlton.¹

Among modern species of *Prunus*, this species is very similar to the thick-leaved *Prunus demissa* (Nutt.) Dietr., which is very prevalent in portions of the xerophytic chaparral formation of California. Knowlton has already noted¹ the similarity of the Mascall specimens to the same western species. It is possible that the poor representation of the species in the Pliocene sediments may be due to the fact that, like its living relative, it preferred the dry, open hillsides where its leaves might only rarely be carried to streams or lakes for possible preservation.

Among the few Tertiary species of *Prunus*, the closest resemblance seems to be with *P. coveus* Chaney from the Crooked River Oligocene,² from which it differs mainly in texture. It is possible, as Chaney suggests,² that the Mascall species merely represents a leaf variation of *P. coveus* due to a less humid habitat. Both the Mascall and Pliocene plant associations indicate much less humid conditions than the Crooked River assemblage.

Occurrence—St. Mary's College, Locality 162; Lafayette Dam, Locality 163; Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., No. 387, Loc. 160; No. 388, Loc. 162; No. 389, Loc. 163.

Genus HETEROMELES Roem.

Heteromeles sp.

(Plate 12, fig. 2)

Only three rather complete but poorly preserved specimens of this species were encountered, at one locality. Its significance lies particularly in the fact that it seems clearly referable to the genus *Heteromeles*, which has not previously been reported in the Tertiary record of North America, and in the ecological conditions which its presence suggests.

The leaves, one of which is figured, are not unlike those of the living species, *H. arbutifolia* Roem. (*Photinia arbutifolia* Lindl.³), the only American representative of the genus. They were evidently coriaceous, as indicated by the indistinct venation and the slight curling of the margin, and were set with equilateral, attenuate teeth which differ from those of the

¹ Knowlton, U. S. Geol. Surv. Bull. 204, 67, 68, pl. 11, figs. 2, 3, 6, 7, 1902.

² Chaney, Carnegie Inst. Wash. Pub. No. 346, pt. IV, 123, 124, pl. 15, figs. 1-4, 6, 1927.

³ Jepson, *Manual of the Flowering Plants of California*, 508, 1925.

modern species only in being more widely spaced. The few details of venation discernible are of the same type as in the living form.

Heteromeles arbutifolia is a rather dominant member of the climax chaparral of the Sierra Nevada and Coast Ranges of California, though it frequently occurs in exposed situations in the redwood border forest. It has been noted by the writer along the Eel River in Humboldt County in an association of typical redwood border species. The fossil species found in association with *Heteromeles* sp., suggest conditions comparable to a redwood border forest supporting a scattered growth of redwoods, surrounded by an open forest of broad-sclerophyll and chaparral species.

Occurrence—Petrified Forest, Locality 150.

Collection—Univ. Calif. Coll. Pal. Bot., Nos. 390, 391, Loc. 150.

Genus AMELANCHIER Medic.

Amelanchier sp.

Only a few incomplete specimens from one locality are referred to this species. The few characters preserved seem to indicate a leaf which is different from any of the others found at the same locality. A comparison with herbarium material seemed to indicate a rather close relationship to the modern *Amelanchier alnifolia* var. *pallida* Jepson, which is characteristic of the more arid portions of the lower Sierra Nevada and Coast Ranges of California. The leaves of this species, as well as the Pliocene form, are entire except for the extreme upper portion, which is marked with rather blunt serrations.

The incompleteness of the material makes comparisons with other Tertiary forms rather difficult. All of the seven previously described species are distinctly more serrate-margined. An examination of Hannibal's specimens from the same locality indicated that he referred similar leaves to the modern *A. alnifolia* Nutt. He states¹ that the species is not common in the Santa Clara beds, and the few specimens in his collections are no more diagnostic in details than those collected by the writer. Chaney's recent revision of the flora also includes *Amelanchier* cf. *alnifolia*,² so that it seems extremely likely that the above identification is valid, in spite of the fact that the species can not be completely described or figured at the present time.

Occurrence—Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., Nos. 392, 393, Loc. 160.

ORDER SAPINDALES

Family ANACARDIACEÆ

Genus RHUS Linné

Rhus. sp.

(Plate 12, fig. 4)

About a half dozen rather incomplete specimens referable to this species have been collected from two localities. They have a general resemblance to several California species of *Rhus*, notably *R. laurina* Nutt. and *R. ovata* Wats. The general shape, as observed in one rather poorly preserved specimen, is ovate-lanceolate, which seems to be intermediate between the ovate form in *R. ovata* and the more lanceolate form in *R. laurina*. The venation

¹ Hannibal, Bull. Torrey Bot. Club, vol. 38, 335, 1911.

² Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 45, 1925.

is very obtuse, as in *R. laurina*, and the finely serrate margin is suggestive of *R. ovata*, which may be either serrate or entire; *R. laurina* was not seen to be serrate at all. Sheet No. 109830 in the herbarium at the University of California indicates clearly the similarity to *R. laurina* while Sheet No. 168785 indicates the resemblance to *R. ovata*.

Not many of the numerous Tertiary species of *Rhus* show much resemblance to the leaf type of *Rhus* sp. or to its modern relatives. *R. menseæ* Cockerell (*R. metopioides* Lesq.) from the Miocene Auriferous gravels¹ differs only slightly in a more ovate shape and an entire margin. A general similarity to *R. merrilli* Chaney from the Crooked River Oligocene² is noted, although the latter has a more open type of venation and is also entire-margined. A closer resemblance is seen with *Chrysobalanus pol-lardiana* Knowlton from the Esmeralda Miocene,³ which presents the same character of base, prominent midrib and secondary venation as the Pliocene species. The reference to *Chrysobalanus* seems rather questionable in view of the present restriction of the genus to the southern portion of Florida, the West Indies and Central America, where its climatic requirements are very different from those which are suggested in the north-temperate assemblage of poplars, willows and oaks in the Esmeralda.

Rhus laurina and *R. ovata* are both characteristic of the climax chaparral of California. When associated with larger forest trees they usually grow in exposed, rather dry situations, which is in accord with the conditions suggested in the associations of the fossil species.

Occurrence—St. Mary's College, Locality 162; Lafayette Dam, Locality 163.

Collection—Univ. Cal. Coll. Pal. Bot., No. 394, Loc. 162; No. 395, Loc. 163.

Family AQUIFOLIACEÆ

Genus ILEX (Tourn.) Linné

Ilex sonomensis Dorf, new species

(Plate 12, figs. 6, 7; plate 13, figs. 1, 2)

A very complete suite of specimens of this species has been collected at two localities, at one of which it is very abundant, at the other only poorly represented by a few rather questionable fragments. Both localities are in the same formation, the Sonoma tuff. The numerous well-preserved specimens from the Petrified Forest locality have made possible a careful study of the variations in size, shape, and marginal characteristics of the species.

Description—Leaves obovate to broadly ovate, narrowing gradually to an acutely cuneate, slightly asymmetrical base, and rather abruptly to a broad, rounded, or even slightly truncate apex; length 5 to about 8 cm.; width 3.1 to 4.2 cm.; average dimensions about 3.3 by 5.8 cm.; midrib straight and firm; petiole thick, enlarged at the base, and up to 9 mm. long; 5 to 8 pairs of alternate to subopposite, slender secondaries, diverging from the midrib at an angle of about 60° near the apex to 85° near the base; occasional secondaries, especially those near the base, decurrent with the midrib; secondary venation camptodrome, the secondaries curving upward and forming a series of loops with those next above and either

¹ Lesquereux, Mus. Comp. Zool. Mem., vol. 6, No. 2, 31, pl. 8, figs. 12, 13, 1878.

² Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. IV, 125, pl. 16, figs. 1, 2, 1927.

³ Knowlton, U. S. Geol. Surv., 21st Ann. Rpt., pt. 2, 216, pl. 30, fig. 19, 1901.

terminating in the marginal teeth near the apex or giving off prominent tertiaries from the lower sides of the loops, which run into the marginal teeth, when present, in the central or lower portions of the blade; when teeth are not present the terminal portions of the secondaries become obscured in the tertiary venation near the border; tertiaries usually prominent, irregularly percurrent near the margin, particularly prominent toward the central portion where they run out from the midrib paralleling the secondaries for a considerable distance, then turn sharply downward and join the secondary at almost a right angle; nervilles forming a distinct fine network; margin remotely spinose-dentate to entire, the teeth attenuate, produced into short spines and directed slightly upward; texture subcoriaceous.

Discussion—The generic determination of this species was not an easy one. It was at first thought to be an oak, perhaps of the prevalent western live-oak group, but a careful study of the herbarium material of all the available oaks at The New York Botanical Garden eliminated *Quercus* as a possible generic reference. A subsequent survey of all the genera of North America whose leaves were even suggestive of the fossil specimens brought out a rather positive reference to *Ilex*, the secondary venation of which is practically identical in most of the leaves examined, even in the case of those whose shape and margin were radically different. The closest resemblance was with *I. brandegeana* Loes. (N. Y. Botanical Garden, sheet No. 118, San Ramon, Durango, Mexico), which has identical venation, the same shape and the same remotely spinose-dentate margin. The type specimens of the species, recently examined at the University of California, were equally similar in most details, differing in a more rounded base.

Among the numerous species of *Ilex* described from the Tertiary of North America there is none with which a close comparison is possible. *I. affinis* Lesquereux from the Green River Eocene,¹ though possessing a similar shape, differs considerably in its less-spinose teeth and in secondary venation. *I. falsani* Sap. and Mar. of the European Pliocene² is more similar in shape and venation but is not known to be even remotely dentate.

The absence of *Ilex sonomensis*, or any other representative of the genus, from all but one of the Pliocene formations of California seems rather significant in view of the total absence of the genus in the modern flora and its former abundance throughout the Tertiary of the regions west of the Rockies. Eight species are reported from the Cretaceous, 4 from the Eocene and 8 from the Miocene. The value of this enumeration depends entirely, of course, on the accuracy of specific and generic determinations. One species, for example, *Ilex leonis* Cockerell from the Florissant Miocene,³ possesses characters which seem to make it referable rather to the genus *Quercus*, of the live-oak type, as is suggested in Lesquereux's original name *I. quercifolia*.⁴ Other species may possibly represent variable leaf forms which might be combined to make fewer authentic species. Nevertheless, such an enumeration does indicate a distinct tendency toward a reduction in the number of species of *Ilex* from the earlier Tertiary to the Pliocene and present. *Ilex sonomensis*, then, seems to represent a relict species in the Pliocene of California, the last representative of the genus to be present in that state.

¹ Lesquereux, U. S. Geol. Surv. Terr., vol. 7, 270, pl. 50, figs. 2, 3, 1878.

² Saporta et Marion, *Végétaux Fossiles de Meximieux*, 294, pl. 36, 1876.

³ Cockerell, Am. Mus. Nat. Hist. Bull., vol. 24, 99, 1908.

⁴ Lesquereux, U. S. Geol. Surv. Terr., vol. 8, 186, pl. 38, figs. 2-5, 1883.

There is a suggestion in the absence of *Ilex sonomensis* from all the other localities that the Sonoma tuff flora, particularly at the Petrified Forest, is somewhat older than the rest. The study of the association at this locality, however, indicates the same general restriction of the redwood forest and its close associates as do the remaining Pliocene localities, in which case the flora merely represents the preservation of a community of slightly different habitat. Such an inference is corroborated by both the petrographic and ecological evidence, which indicate subaerial preservation of an upland association.

Occurrence—Petrified Forest, Locality 150; Santa Rosa, Locality 154.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 396, 397, 398, 399, 400, 401, 402, Loc. 150.

ORDER RHAMNALES

Family RHAMNACEÆ

Genus CEANOOTHUS Linné

Ceanothus chaneyi Dorf, new species

(Plate 13, figs. 3, 4)

Several rather complete specimens from one locality seem referable to the genus *Ceanothus*. Although the venation is not completely or clearly shown, enough is seen to make comparisons with previously described species possible and thereby justify the reference to a new species. The description is based on the two specimens figured.

Description—Leaves ovate to lanceolate-ovate, gradually narrowing to an acutely rounded, blunt, apex and a broadly cuneate base; length 4.4 to 5.5 cm.; width 2 to 2.6 cm.; petiole thin but firm, up to 10 mm. long; midrib thin, straight or slightly curved, with a pair of prominent secondaries branching off at or slightly above the base at an acute angle, curving slightly upward and terminating in the obscure network near the margin slightly above the middle of the blade; other secondaries much less prominent, diverging at more obtuse angles and looping upward indistinctly near the margin; 3 or 4 pairs of stout tertiaries given off from the abaxial sides of the basal secondaries, curving obtusely outward and upward near the margin; tertiary venation obscure; margin apparently entire; texture rather thin but firm.

Discussion—A comparison of the fossil specimens with herbarium material of the numerous western species of *Ceanothus* clearly identifies them as of rather close relationship to the entire-leaved form, *Ceanothus integririmus* H. and A. The tendency in the modern leaves of this species seems rather toward more acute and longer basal secondaries, though some have been observed which are essentially similar to those in the Pliocene specimens.

The status of *Ceanothus* in the Tertiary fossil record of the west is far from satisfactory. Chaney has already pointed out¹ the probability of the reference of several species of other genera to *Ceanothus*, notably *Paliurus colombi* Heer,² *Zizyphus meekii* Lesquereux,³ *Z. paliurifolius* Knowlton,⁴

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. IV, 129, 1927.

² Lesquereux, U. S. Geol. Surv. Terr., vol. 7, 273, pl. 50, figs. 13-17, 1878.

³ Lesquereux, op. cit., 275, pl. 51, figs. 10-14.

⁴ Knowlton, U. S. Geol. Surv. Prof. Pap. 101, 272, pl. 47, figs. 1-4, 1918.

Cinnamomum dilleri Knowlton¹ and *Ficus mensæ* Cockerell,² in view of the temperate distribution of the genus *Ceanothus* and the tropical or subtropical range of the others, as well as the close identity of the leaves of those species to those of *Ceanothus*.

Only two species from the Tertiary of North America have been referred to *Ceanothus*. The Bridge Creek form, *C. blakei* Chaney³ differs notably from the Pliocene species in venation, shape and margin, whereas the Canadian Oligocene form, *Ceanothus*? sp. Dawson,⁴ bears a marked resemblance in shape and character of the basal secondaries but is obscure in other significant details. An even closer resemblance is seen with the figured specimens of *Ficus mensæ*, mentioned above, from the Miocene Auriferous gravels. It is possible that our species might prove identical if a more complete suite of leaves of both species were obtained.

Hannibal's original collection from the same Pliocene locality does not include any species of *Ceanothus*. A recent examination of his type specimens at Stanford University has convinced the writer that the specimens referred to *Cornus glabrata* Benth. might better be placed in *Ceanothus chaneyi*. Hannibal clearly states⁵ that the leaves show "a pair of strong lateral veins near the base" which was quite unlike most of the herbarium material of *Cornus* which he had examined. Chaney, in his recent revision⁶ of Hannibal's material, clearly recognized a species of *Ceanothus* of the *integerrimus* type.

Ceanothus integerrimus is an important species in the chaparral and as an undergrowth shrub in the coniferous forest of California, particularly in the Sierra Nevada. The association of *C. chaneyi* with other chaparral species and several Sierran conifers suggests a somewhat similar habitat in the Pliocene forests.

This species is named in honor of Dr. R. W. Chaney, Research Associate of Carnegie Institution of Washington.

Occurrence—Calabazas Canyon, Locality 160.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 403, 404, Loc. 160.

ORDER UMBELLALES

Family CORNACEÆ

Genus GARRYA Dougl.

Garrya masoni Dorf, new species

(Plate 13, fig. 5)

Leaves referable to this species have been collected from two localities, at one of which it is represented by only a single specimen, at the other by several well-preserved impressions and numerous fragments. The description is based on the specimens from the Coalinga locality, the best of which is figured.

Description—Leaves ovate-lanceolate to oval, broadest at or just above the middle, narrowing gradually to an obtusely acuminate base and apex; length from 7 to about 11 cm.; width from 3.0 to 3.8 cm. (figured specimen

¹ Knowlton, U. S. Geol. Surv., 20th Ann. Rpt. pt. 3, 47, pl. 4, fig. 1, 1900.

² Lesquereux, Mus. Comp. Zool. Mem., vol. 6, No. 2, 18, pl. 4, figs. 10, 11, 1878 (described and figured as *Ficus microphylla* Lesq.).

³ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. IV, 128, pl. 16, figs. 4, 6-9, 1927.

⁴ Dawson, Roy. Soc. Can. Trans., vol. 8, sec. 4, 84, text-fig. 14, 1891.

⁵ Hannibal, Bull. Torrey Bot. Club, vol. 38, 338, 1911.

⁶ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. II, 45, 1925.

above average); petiole not completely preserved, apparently very stout; midrib stout, curving slightly above the base and recurving toward the apex; secondaries in 6 to 8 pairs, stout, irregularly alternate, diverging from the midrib at varying angles, though mainly acute; all of the secondaries flexuose, curving upward and forking near the margin, or in some cases close to the midrib, giving rise to two branches of equal size, which may bifurcate again; extremities of secondaries, or their branches, curving upward and joining the branch next above in a series of well-defined loops; tertiaries distinct in some portions of leaf, forming irregular quadrangular areas between the basal portion of the secondaries and the midrib and more irregular meshes between the terminal portions of the secondaries, or their branches; margin entire and undulate and usually curled downward, indicating a coriaceous texture.

Discussion—The leaves of this species were first thought to represent aberrant forms of *Fraxinus* foliage. A comparison with all available herbarium material of *Fraxinus* at the University of California made such a reference untenable. After consulting as many genera as possible, whose leaf form approximated the specimens, the genus *Garrya* was examined at the suggestion of H. L. Mason, of the Department of Botany at the University of California. A close similarity, particularly in the shape and the peculiar character of the secondary branching, was noted with several western species, particularly *Garrya elliptica* Dougl. and *Garrya fremontii* Torr. Herbarium specimens showed that the leaves of both these species are somewhat smaller in size, though it is not unreasonable to expect to find specimens even larger than the leaf figured, where the growth of the shrubs is rapid.¹ The leaves of *Garrya elliptica* in sheet No. 306774, at the University of California, showed the same unusual branching of the flexuose secondaries and similar midrib, texture and curling of the margin, but differed slightly in a broader shape and in a more obtuse base. Leaves of *Garrya fremontii*, collected by Mason in a chaparral association in Alameda County, California, differed only in being somewhat smaller in average size. Specimens of *Garrya pallida* Eastw. (*G. flavescens* Wats.), in sheet No. 106055, showed similar venation and textural characteristics, differing only in its smaller size and slightly more acute base.

The genus *Garrya* has not been previously reported in the fossil record. No other figured Tertiary species have been noted with which a comparison is possible.

Garrya elliptica and *G. fremontii* are both members of the xerophytic chaparral of the semi-arid slopes of California.² The former is more characteristic of the lower elevations of the Coast Ranges, while the latter is more typical of the inner Coast Ranges and Sierra Nevada, though it reaches the coastal portions in the Sierra Madre. Mason has recently informed the writer of its occurrence in the xerophytic forest assemblage on Cedar Mountain, on the inner side of the Mount Hamilton Range.³ Here it is associated with *Quercus douglasii* and *Pinus sabiniana*, which are characteristic xerophytic types of the sparsely forested slopes of the interior. The Pliocene associations of *Garrya masoni* are mainly of semi-arid aspect and indicate a somewhat similar habitat as that in which its modern correlates live.

¹ Mason, Written communication, Oct. 22, 1929.

² Cooper, Carnegie Inst. Wash. Pub. No. 319, 119, 1922.

³ Mason, Written communication, Oct. 22, 1929.

The species is named in honor of Mr. H. L. Mason, of the Department of Botany, of the University of California.

Occurrence—Bennett Valley, Locality 152; Coalinga, Locality 164.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 405, 406, 407, Loc. 164.

ORDER GENTIANALES

Family OLEACEÆ

Genus *FRAXINUS* (Tourn.) Linné

Fraxinus caudata Dorf, new species

(Plate 13, figs. 6, 7, 8)

This species is well represented by numerous rather complete specimens from five localities. No one specimen is complete in all details but all of the important characters are apparent in the entire suite.

Description—Leaves ovate-lanceolate, broadest at or just below the middle, gradually narrowing to a caudate-acuminate apex and an asymmetrical acutely cuneate base; length from 8.2 to 10.6 cm. (estimated); width from 2.5 to 3.8 cm.; petiole short and stout, about 4 mm. long; midrib rather stout, straight or slightly curved below the middle and usually recurved toward the apex; secondaries in 6 to 9 pairs, irregularly subopposite to alternate, diverging from the midrib at an obtuse angle, approaching 90° on one side of the midrib and usually at a more acute angle on the opposite side; most of the secondaries forking near the margin or in some cases as much as halfway down toward the midrib, the main branches curling uniformly upward and outward, forming distinct loops with the secondaries next above or their lower branches; tertiaries forming an indistinct network, usually poorly preserved; one set of tertiaries rather prominently emerging from the midrib between the secondaries, to which they are parallel or subparallel, and continuing toward the margin where they become less and less distinct, joining the tertiaries in the marginal loops, or in other cases becoming more quickly obscured in the tertiary venation between the secondaries; margin entire and slightly undulate in some specimens; texture rather sub-coriaceous, as indicated by the obscured tertiary venation and the undulate margins.

Discussion—The leaves of this species belong to the entire, ovate-lanceolate types whose generic and specific determinations are perhaps the most difficult of all leaf forms. For purely stratigraphic purposes they might indeed be referred to any one of half a dozen or more genera without detracting from their usefulness for correlation. When the more biologic or ecologic considerations are attempted, on the other hand, it is obvious that a more definite determination must be made. In an attempt to identify the generic characters most accurately the writer has studied herbarium material of all the available species from western North America whose leaf form approached even remotely that of the species in question.

Beside the forms which had already been studied in connection with the determination of other Pliocene forms the western species of the following genera were carefully examined: *Ptelea*, *Osmoronia*, *Rhododendron*, *Fraxinus*, *Cephalanthus*, *Sapindus*, *Persea*, *Rhamnus*, *Dirca*, *Cornus*, *Calycanthus*, *Styrax* and *Juglans*. Although many of the species had entire, ovate-lanceolate leaves, most of them were found to possess radical differences in venation and texture, together with minor, though easily discernible, differences in shape, base and apex. The closest resemblance

was with *Fraxinus oregona* Nutt., a widely distributed western form, whose leaves are made up of entire, ovate-lanceolate leaflets with short petioles, unequilateral bases, slightly caudate tips and unsymmetrical secondary venation. The modern tendency seems rather toward strictly ovate rather than ovate-lanceolate shapes, though many specimens were encountered which were equally lanceolate, or even more lanceolate, than *F. caudata*. The details and minor irregularities in the secondary venation were essentially alike in both *F. oregona* and the fossil species. Herbarium sheet No. 150298 at the Field Museum and sheets Nos. 34902 and 154169 at the University of California contain leaflets which were not easily distinguishable from most of the fossil specimens.

Most of the other species of *Fraxinus* from the Tertiary of North America are typically serrate, whereas no serrate-margined forms have been observed in the Pliocene species. The entire-margined leaves of *F. denticulata* Heer from the Bridge Creek Oligocene¹ are not unlike some of the Pliocene specimens, though they differ somewhat in shape and basal characters and are elsewhere known to be distinctly dentate.² A general similarity was suggested in the figures of *Persea pseudo-carolinensis* Lesquereux from the Miocene Auriferous gravels³ and *Laurus similis* Knowlton from the Eagle Creek Oligocene⁴ and Latah Miocene.⁵ An examination of the type specimens of these species at the United States National Museum, however, brought out major differences in venation and details of shape.

Fraxinus oregona is widely distributed from southern British Columbia through western Washington and Oregon to the Coast Ranges and Sierra Nevada foothills of California. It is typically a stream-border type of the more open forests. The association of *F. caudata* with such stream-border types as *Alnus*, *Platanus*, *Salix* and *Populus* indicates similar habitat requirements for the Pliocene form.

Occurrence—Garberville, Localities 155, 156; Santa Rosa, Locality 154; Lafayette Dam, Locality 163; Coalinga, Locality 164.

Collection—Univ. Calif. Coll. Pal. Bot., Cotypes, Nos. 408, 409, 410, Loc. 156; Cotype, No. 411, Loc. 164; No. 412, Loc. 154.

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. IV, 132, pl. 19, figs. 5-7, 1927.

² Heer, Fl. Foss. Arct., vol. 1, 118, pl. 16, fig. 4, 1868.

³ Lesquereux, Mus. Comp. Zool. Mem., vol. 6, No. 2, 19, pl. 7, figs. 1, 2, 1878.

⁴ Chaney, Walker Mus. Contr., vol. 2, No. 5, 173, 1920.

⁵ Knowlton, U. S. Geol. Surv. Prof. Pap. 140, 41, pl. 23, figs. 4-6; pl. 24, fig. 2, 1926.



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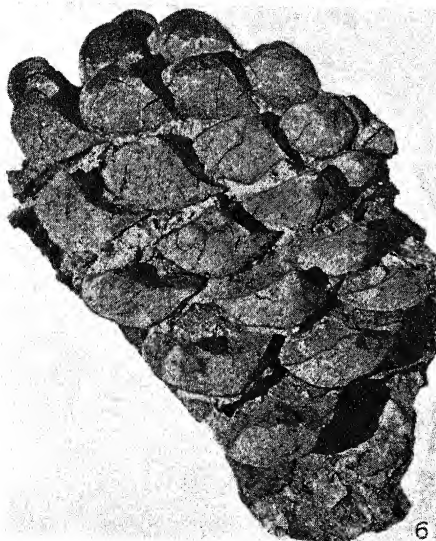
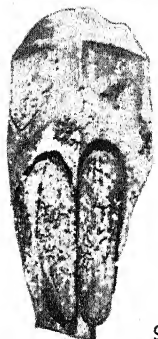
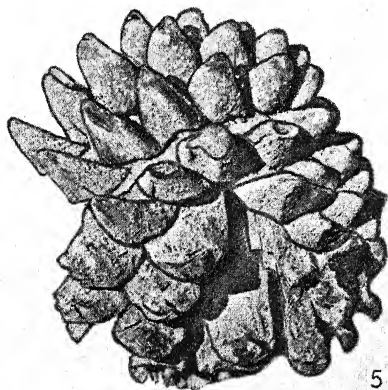
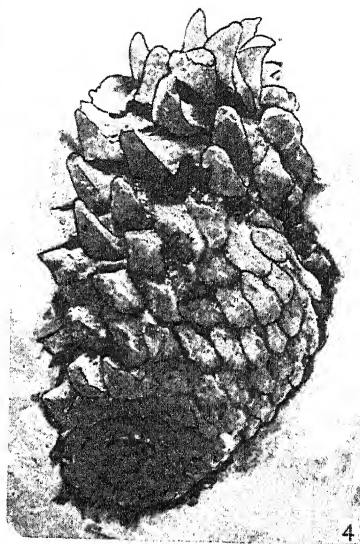
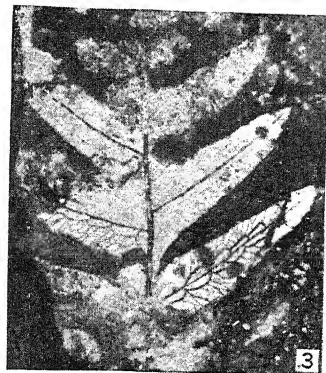
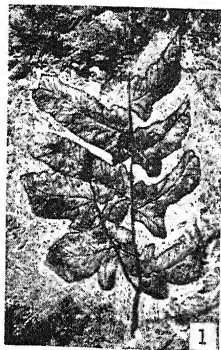
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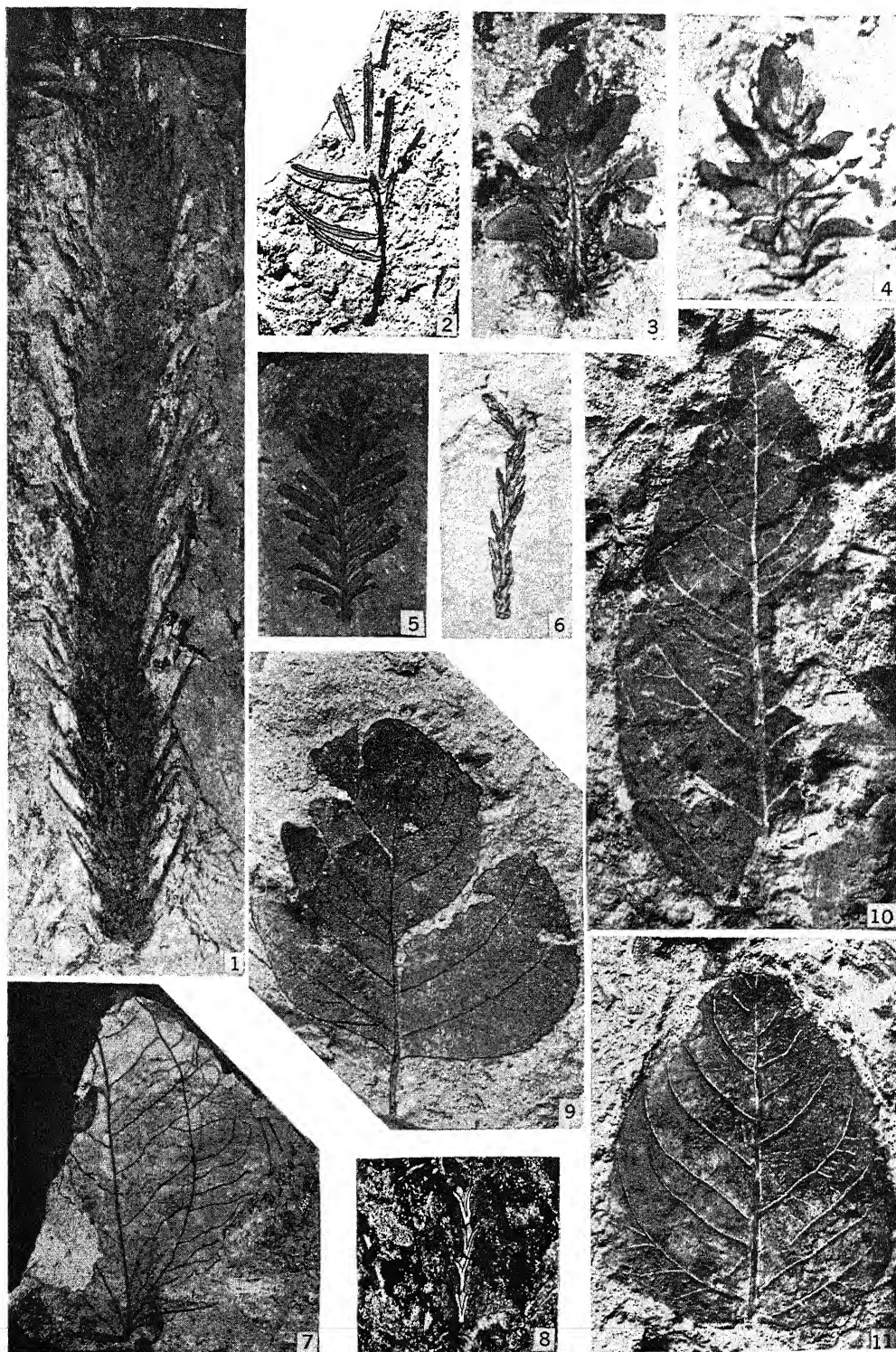
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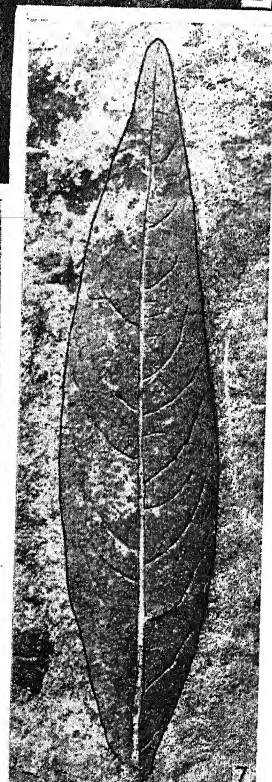
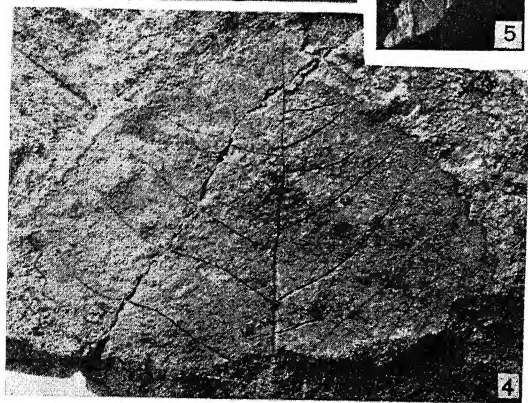
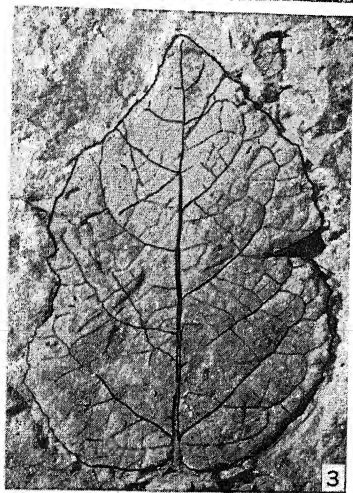
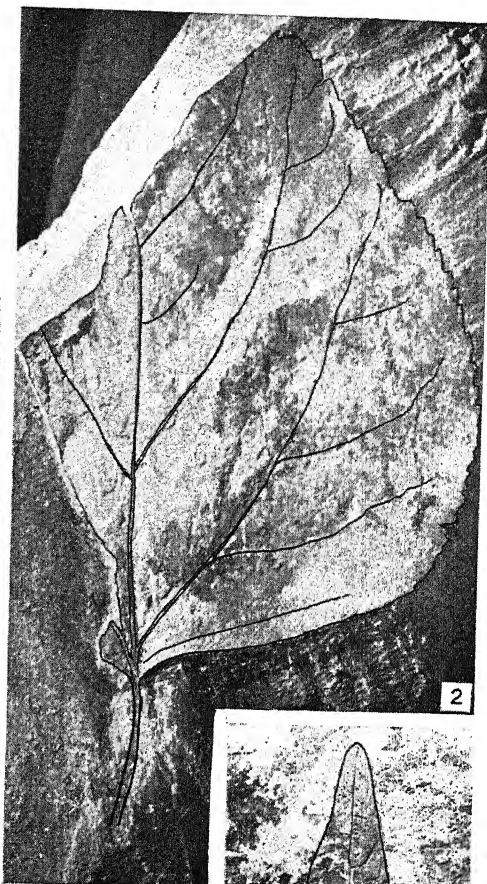
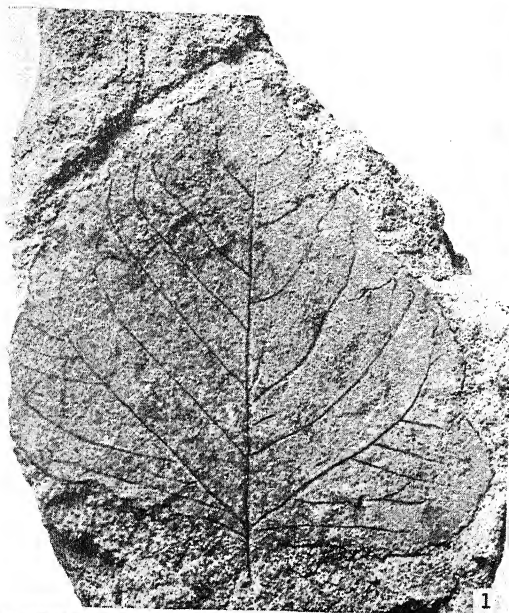
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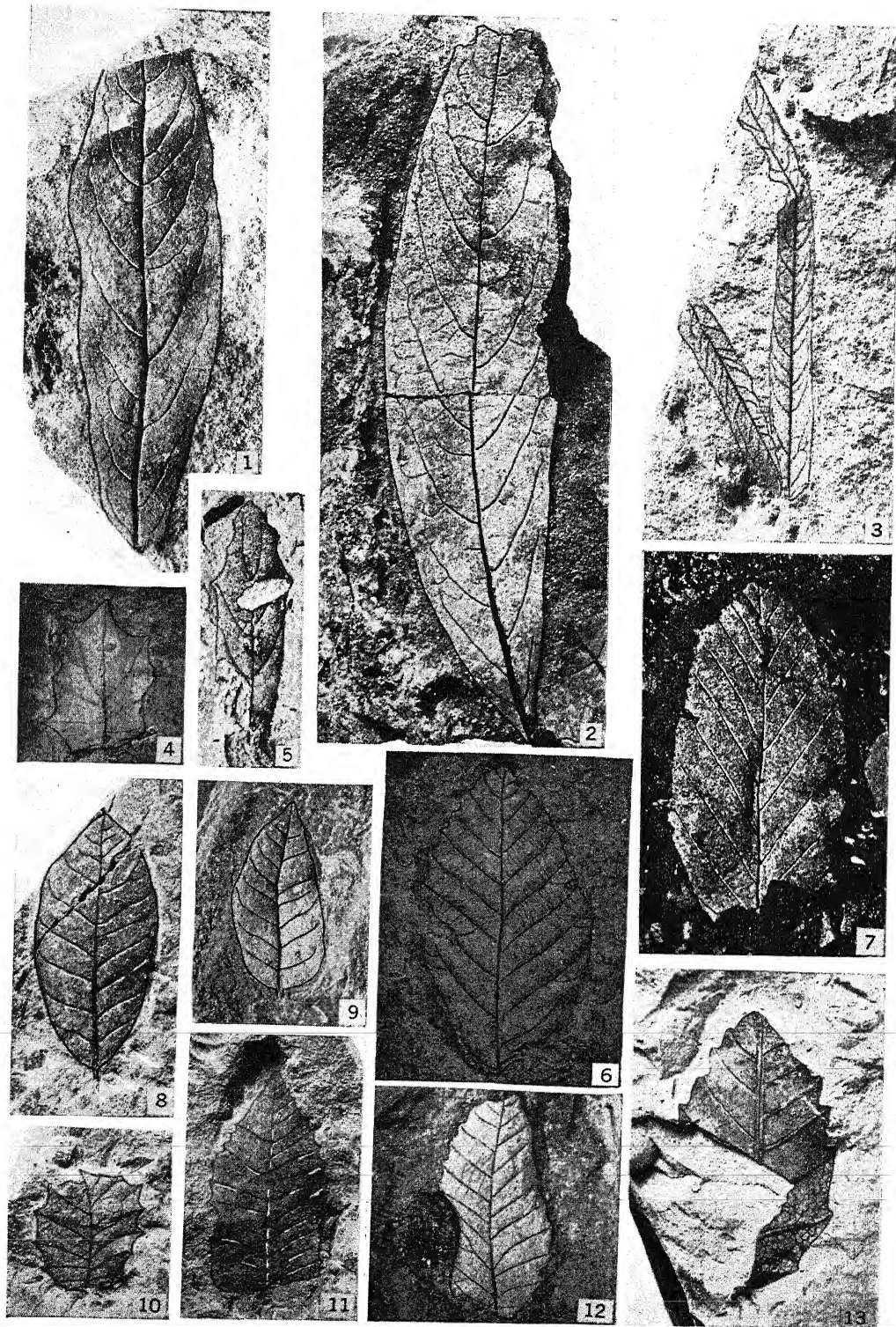
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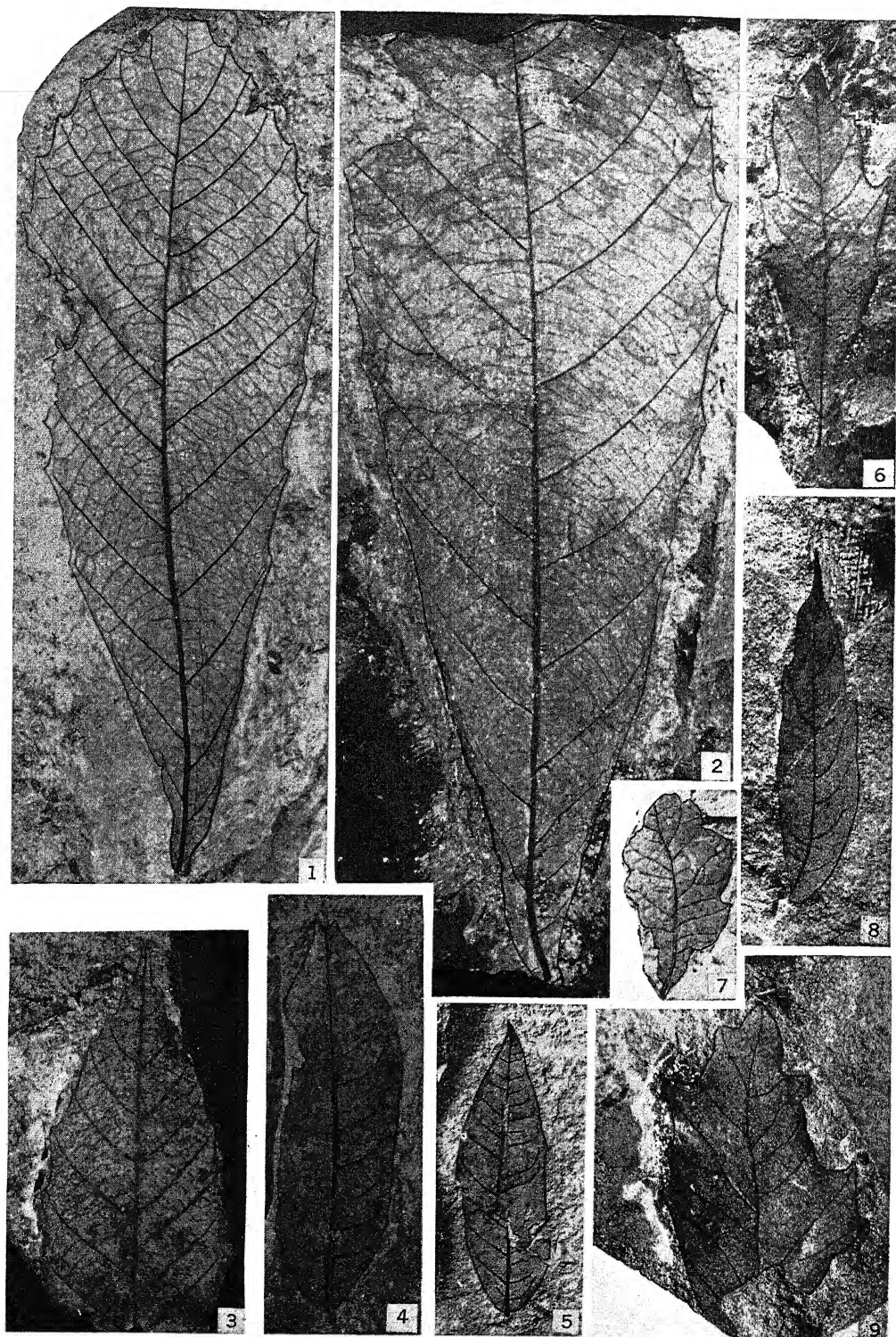
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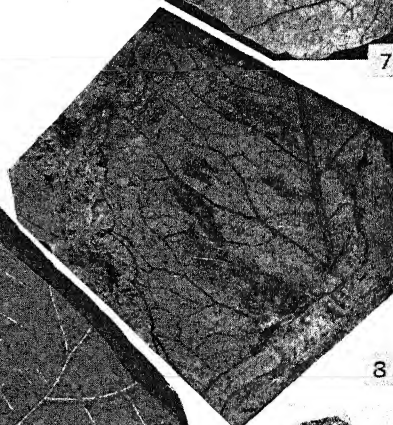
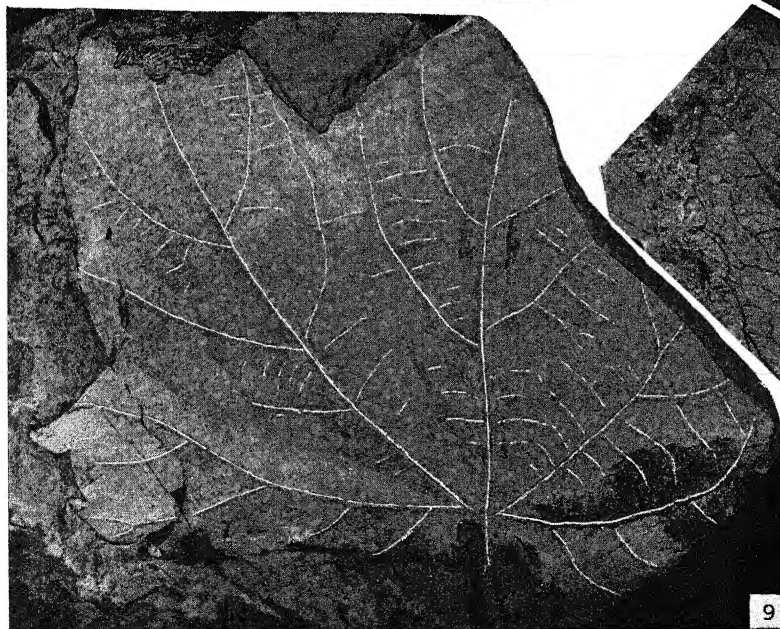
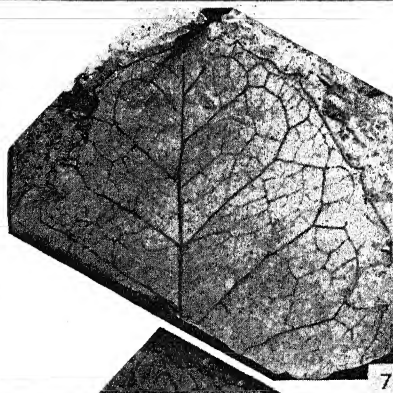
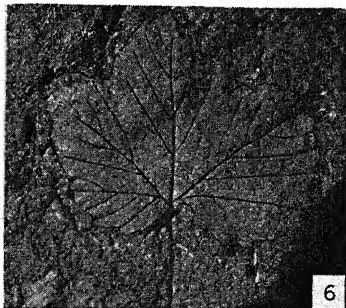
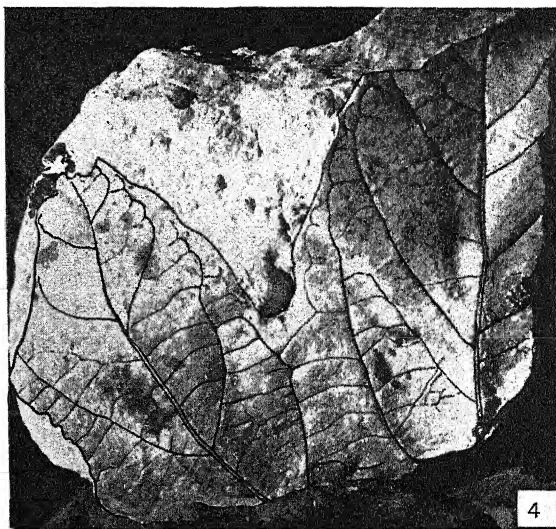
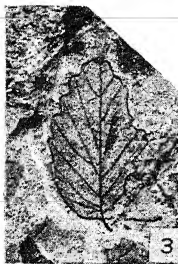
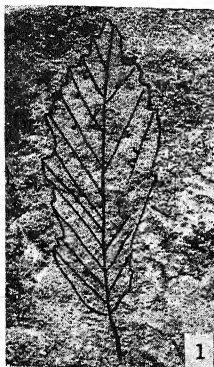
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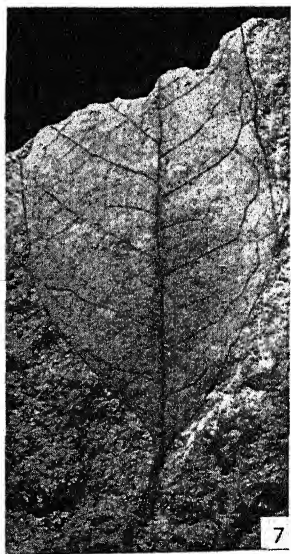
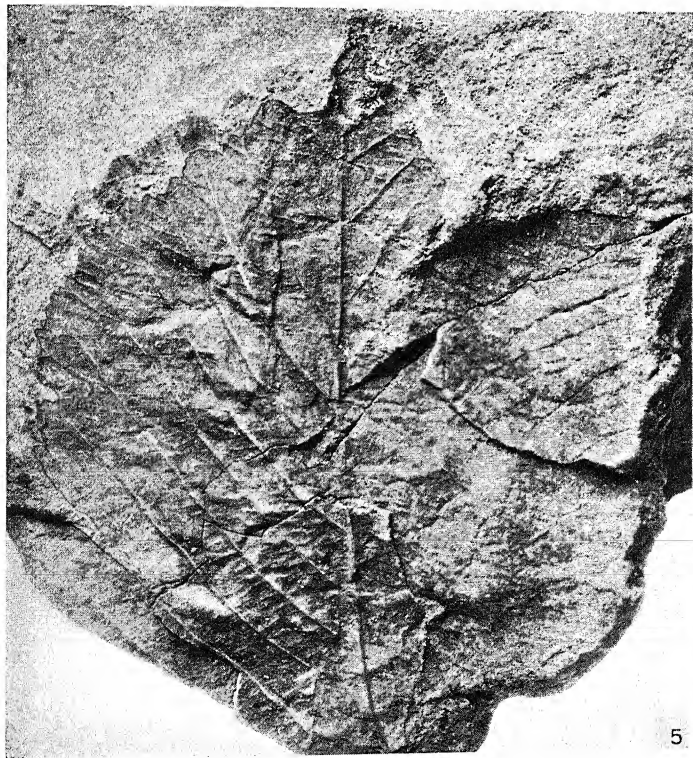
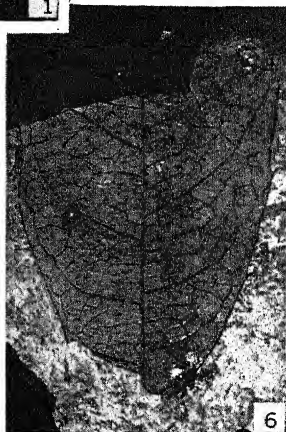
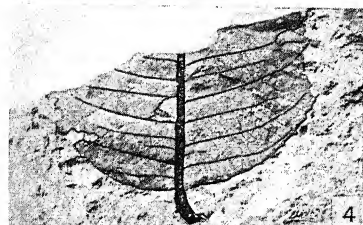
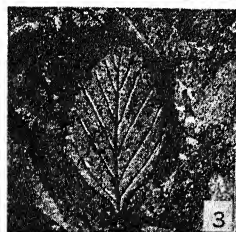
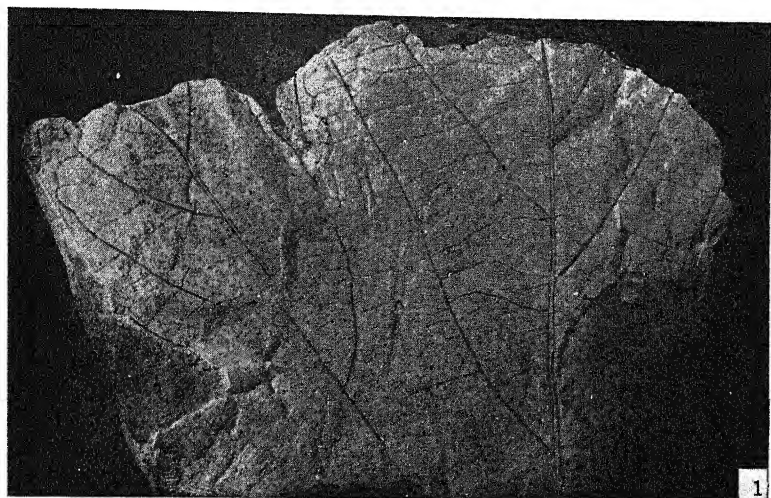
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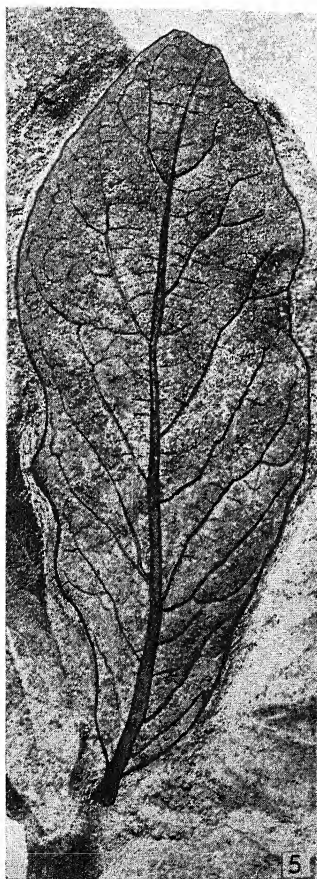
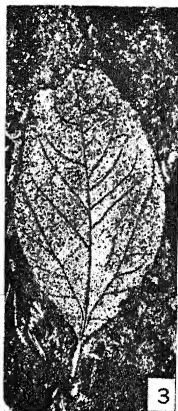
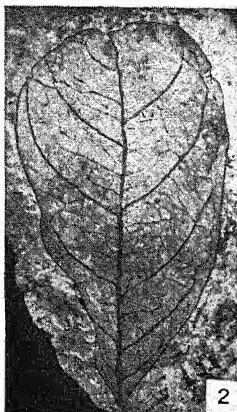
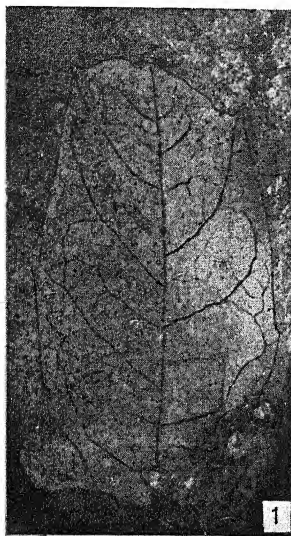
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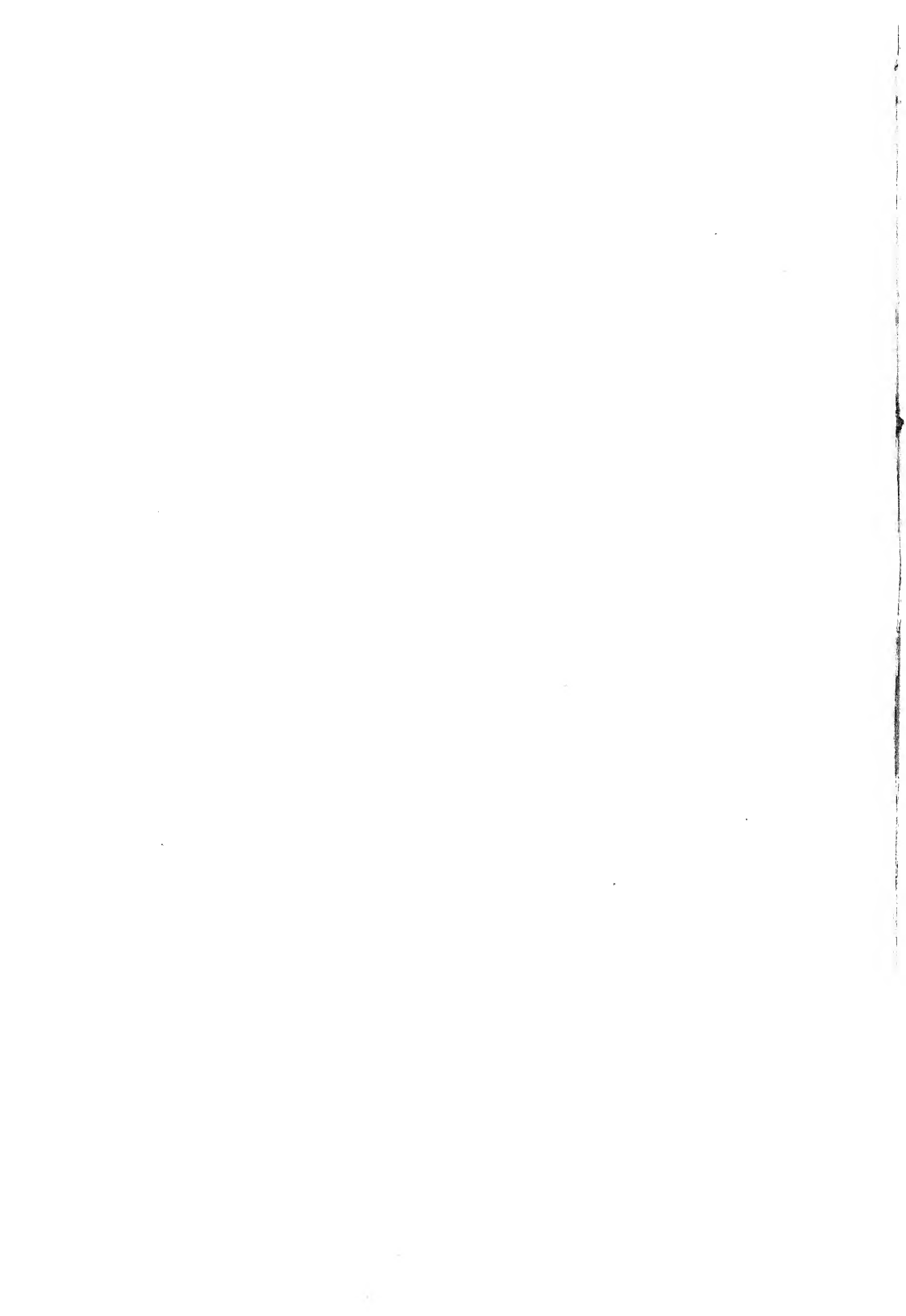
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II

WOODS FROM THE RICARDO PLIOCENE OF
LAST CHANCE GULCH, CALIFORNIA

By IRMA E. WEBBER

With five plates

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WOODS FROM THE RICARDO PLIOCENE OF LAST CHANCE GULCH, CALIFORNIA

INTRODUCTION

This paper is based upon a field and laboratory study of petrified wood from the lower Pliocene of the Mohave Desert. Of the three collections available for study, two are in the Museum of Paleontology of the University of California; the larger of these was collected by Miss Annie M. Alexander, Miss Louise Kellogg and Ralph W. Chaney in 1924; the other was secured by Dr. J. C. Merriam and his associates some years ago. The third collection was placed at the disposal of the writer by Mr. C. L. Hill of the California Forest Experiment Station.

GEOLOGICAL OCCURRENCE

Fossil wood is abundantly represented in the Ricardo Pliocene beds 3 miles north of the entrance to Last Chance Gulch in the El Paso Mountains, Searles Lake Quadrangle, U. S. Geological Survey, section 8, T.29S., R.38E., Mount Diablo base and meridian. This locality is approximately 4 miles northeast of Red Rock Canyon. The occurrence of petrified tree trunks in these beds has been mentioned by Stock and Furlong.¹

The deposits containing the fossil woods are similar in their stratigraphic position and lithologic characters to those described by C. L. Baker² in the Red Rock Canyon region. These deposits, those in the Barstow syncline, and other exposures, which are widely spread over the Mohave area, were referred by Baker to the Rosamond series, which he considered to be of upper Miocene age. In 1912, Baker³ briefly described the deposits in Last Chance Gulch, and likewise referred them to the Rosamond series. Following the discovery that the fauna from the beds in Red Rock Canyon is distinctly later than that of the upper Miocene Barstow deposits, J. C. Merriam⁴ in 1919 described numerous mammalian forms from the Red Rock Canyon section as representing the Ricardo Pliocene. This terminology has been continued by Stock and Furlong⁵ in their paper dealing with the

¹ Stock, Chester, and E. L. Furlong, Univ. Calif. Pub. Bull. Dept. Geol., vol. 16, No. 2, 43-60, 1926.

² Baker, C. L., Univ. Calif. Pub. Bull. Dept. Geol., vol. 6, No. 15, 333-383, 1911.

³ *Op. cit.*, vol. 7, No. 6, 117-142, 1912.

⁴ Merriam, John C., Univ. Calif. Pub. Bull. Dept. Geol., vol. 11, No. 5, 437a-437e, 438-585, 1919.

⁵ *Op. cit.*

fauna of Last Chance Gulch, in which they state that the Ricardo stage may occupy a position between that of the Republican River, which is regarded as latest Miocene or earliest Pliocene, and the slightly later stage of Upper Snake Creek.

The mammalian fauna which has been described from the Ricardo deposits represents one of the largest and most important assemblages from the Pliocene of western North America. Canid, rhinocerotid, proboscidean and artiodactyl remains have been reported from Last Chance Gulch. Additional forms are known from the deposits in Red Rock Canyon. In Last Chance Gulch, mammalian remains have been reported both above and below the horizon containing the fossil tree trunks. Canid and rhinocerotid remains were found approximately 25 feet higher in the section, in the immediate vicinity of the locality where the petrified trees occur.

In the portion of his paper dealing with the relation of the Ricardo fauna to its environment, J. C. Merriam¹ states that a partly open, level region would provide a suitable environment for the forms represented, as none of them must necessarily be regarded as representative of a forest or mountain assemblage carried out to the plains. The large representation of grazing animals indicates conditions favorable for a heavier growth of grass than is found in the region today. This would suggest less extreme aridity than now prevails on the western border of the Mohave Desert, although there are no elements in the fauna which require conditions radically different from those now found in the region.

Up to this time, there have been no publications dealing with the Ricardo flora. This paper presents the results of a study made under the direction of Dr. R. W. Chaney, to whom I wish to express my gratitude.

Because of the excellent state of preservation of the wood, the general types were easily recognized with a hand lens; however, accurate generic determinations could not be made without higher magnification. Accordingly, wood of each type was selected for sectioning, most of the sections were prepared at the Osborn Botanical Laboratory, through the courtesy of Dr. George R. Wieland, and additional ones were prepared by Mr. V. L. VanderHoof at the University of California. Microscopic examination of this wood disclosed the presence of 6 species of woody plants and several types of fungi, which are described below. Four species, all of which have been described as new, have been designated as follows: *Palmoxylon mohavensis*, *Pinus kelloggi*, *Quercus ricardensis*, *Robinia alexanderi*. In addition there

¹ *Op. cit.*

in a species of *Cupressus*, which is not assigned a specific name, and material representing an unknown dicotyledon.

Robinia and *Palmoxylon* form a large percentage of the specimens in the collections and are the only species which were observed in the field. All of the trunks exposed in the area known as the Saltdale Petrified Forest represent *Robinia*; approximately two-thirds of these trunks are standing. The largest standing stump is about 4½ feet in diameter at the base and 8 feet tall. Fallen trunks range to 12 feet in length. Root crowns up to 5 feet in diameter, single stumps some of which are branched, and twin stumps are represented. Much of the rock exposed is filled with abundant small roots which are undoubtedly related to the trunks. A group of *Palmoxylon* roots, apparently representing one tree, were observed near some of the *Robinia* trunks.

HISTOLOGICAL DESCRIPTIONS

In view of the fact that only wood structures are preserved, it has seemed proper to consider these species as new, even though a close relationship to modern species of their genera is apparent in the case of each.

Palmoxylon mohavensis new species

(Plate 1, fig. 4; plate 2, fig. 4; plate 3, fig. 4)

Palmoxylon Schenk, Engler's bot. Jahrb. vol. 3, 486, 1882.

Transverse Section—Ground mass parenchyma, the cells thin walled, mostly hexagonal, about 17.5 to 52.5 μ in diameter; large intercellular spaces absent. Fibro-vascular bundles distant 0 to 2400 μ , ovoid or rather irregular in shape, mostly about 1350 μ long and about 1425 μ wide; posterior sclerenchymatous arch absent. Fiber part of the bundle much larger than the vascular part, about 675 to 1125 μ long and 855 to 1575 μ wide, turban shaped, forming a shallow arch where joined to vascular part of the bundle. Fibers 14 to 17.5 μ in diameter; the walls very thick, with simple pits. Vascular bundles collateral, with 3 to 7 vessels, mostly with two larger broadly oval or round pores, one at either shoulder of the bundle, the smaller pores commonly oval or angular, in front of or between the larger ones. Phloem fragmentary: sieve tubes round to hexagonal, from 38.5 to 41 μ in diameter, thin walled; companion cells oblong to hexagonal, about 14 μ in diameter. Auxiliary sclerenchyma bundles quite numerous, without bundle sheath; round, from 120 to 150 μ in diameter; the cells mostly hexagonal, about 14 to 21 μ in diameter, thick walled.

Longitudinal Section—Vessel walls with annular thickening, character of pitting not visible.

Of the fossil palm woods previously reported from North America, the following have been described in detail:

Cretaceous Species:

- Palmoxylon cliffwoodensis* Berry,¹ Magothy, Cliffwood, New Jersey
- Palmoxylon anchorus* Stevens,² Monmouth, Seabright, New Jersey
- Palmoxylon cheyennense*, Wieland,³ Pierre, South of Mouth of Battle Creek, South Dakota
- Palmoxylon texense* Stenzel,⁴ Texas
- Palmoxylon astron verum* Stenzel,⁴ Tlacolula, Mexico
- Palmoxylon tenue* Stenzel,⁴ Tlacolula, Mexico
- Palmoxylon cellulolum* Knowlton,⁴ Tlacolula, Mexico

Tertiary Species:

- Palmoxylon cellulolum* Knowlton,⁴ Oligocene, Mississippi, Tertiary: Rapides Parish, Louisiana
- Palmoxylon quenstedti* Felix,⁴ Eocene, Rapides Parish, Louisiana
- Palmoxylon cannoni* Stevens,³ Eocene, Suburbs of Denver, Colorado
- Palmoxylon ovatum* Stenzel,⁴ Eocene, Washington, Mississippi
- Palmoxylon mississippense* Stenzel,⁴ Eocene, Washington, Mississippi
- Palmoxylon remotum* Stenzel,⁴ Eocene, Washington, Mississippi

Of these species, *Palmoxylon anchorus*, *P. cannoni*, *P. cellulolum*, *P. cliffwoodensis*, *P. mississippense*, *P. remotum* and *P. tenue* differ from the California species in that they lack auxiliary sclerenchyma bundles. The remaining species possess such bundles, but *P. texense* has very loose ground tissue in contrast to the rather dense fundamental tissue of the Ricardo species; the bundles in *P. ovatum*, *P. astron verum* and *P. cheyennense* are characterized by a posterior sclerenchymatous arch, which is lacking in the Pliocene species; and the fibrous part of the bundles of *P. quenstedti* differs in shape from that of the California species. In addition, other more or less marked differences in anatomical structure are noted, but those which have been pointed out are sufficient to indicate that the California species is distinct from the previously described North American species.

The present-day occurrence of a native palm, *Washingtonia filifera* Wendl., in California at once suggested the possibility that the Pliocene and living species might be the same or at least similar. Histological comparison of the fossil specimens with wood of *Washingtonia* showed the species to be different. *Washingtonia* wood lacks auxiliary sclerenchyma bundles; its ground tissue is composed of larger cells and its fibro-vascular bundles are on the average somewhat smaller and with larger, thinner-walled bast fibers than those of the Pliocene species. Since *Pinus cem-broides*, *Quercus agrifolia* and *Cupressus forbesii* now range into Lower California where palm genera other than *Washingtonia* occur, *Palmoxylon mohavensis* may be more closely related to some living palm than to *Washingtonia filifera*.

Palm roots are represented in the collections by specimens with the cortex preserved as well as by a number of fragments of steles. The macroscopic characteristics of the better specimens are indicated in table 1.

¹ Berry, E. W., Amer. Jour. Sci., Ser. 4, vol. 41, 193-197, 1916.

² Stevens, N. E., Amer. Jour. Sci., Ser. 4, vol. 34, 421-436, 1912.

³ Stevens, N. E., Amer. Jour. Sci., Ser. 5, vol. 1, 431-443, 1912.

⁴ Stenzel, K. G., Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, Band 16, Heft 4, 1-182, 1904.

TABLE 1—*Macroscopic characteristics of Palmoxyylon mohavensis* root specimens

Terminal diameters of specimen	Corresponding diameters of stele	Length of specimen	Number of branch roots present	Character of surface
mm. 8 by 6.5 9 by 9	mm. 4.5 by 4.5 5.5 by 5	mm. 45	0	Smooth
9.5 by 8.5 10 by 10	4.5 by 4.5 5.5 by 5	34	2	Smooth
11 by 7 14.5 by 7	6.5 by 5 7.5 by 4	48	0	Wrinkled
13 by 7 13 by 6	7 by 3 5.5 by 4.5	30	0	Rough
12 by 8 13 by 7	6.5 by 5 5.5 by 4.5	32	2	Smooth
11 by 9 16 by 12	Not dis- tinguishable	47	3	Wrinkled
14 by 6 15 by 7	7 by 2.5 6 by 3	26	0	Smooth

The structure of the specimen chosen for sectioning is fairly well preserved in the stele and inner part of the cortex, but is not visible in the peripheral cell layers. According to Drabble's¹ terminology, the outer limiting layer and outer cortex are missing, but all three zones of the inner cortex, the endodermis and the stele are present. The tissues preserved are described in the order found from the periphery to the center.

INNER CORTEX

Outer Zone—Collenchyma forming a band from 120 to 375 μ wide. The cells in cross-section round to hexagonal, mostly hexagonal, from 21 to 49 μ in diameter, the lumina large, cell walls medium, thickened somewhat at the corners; in longitudinal section 120 to 180 μ high, the walls with simple pits about 3 μ in diameter.

Middle Zone—Cortical parenchyma forming a band 420 to 1650 μ thick. Parenchyma cells in cross-section round, oval or hexagonal, greatest diameter from 38.8 to 87.5 μ , the walls thin; in longitudinal section hexagonal to oblong, 35 to 240 μ high. Intercellular spaces common, intercellular passages abundant, irregular in shape, maximum diameter in cross-section 120 to 375 μ .

Inner Zone—Stone cells form two inner bands of cells. The outer band of stone cells 2 to 4 cells wide; the cells in cross-section mostly hexagonal, from 49 to 84 μ in diameter, the walls chiefly about 17.5 μ thick with numerous, conspicuous simple pits; in longitudinal section square to hexagonal, 31.5 to 70 μ high, with numerous simple pits about 2.5 μ in diameter. Inner band of stone cells 2 to 4 cells wide. The cells with radially shortened

¹ Drabble, Eric., Trans. Linn. Soc., Ser. 2 Bot., vol. 6, 427-487, 1905.

diameters, in cross-section oblong to hexagonal, about 35 to 87.5 μ by 21 to 28 μ , the walls about 7 μ thick with numerous simple pits about 2.5 μ in diameter; in longitudinal section square to hexagonal or oblong, from 17.5 to 52.5 μ high.

Endodermis—The cells in cross-section U-shaped, radial diameter from 17.5 to 24.5 μ , tangential diameter from 14 to 21 μ , the inner and radial walls considerably thicker than the outer wall; in longitudinal section oblong, from 66.5 to 119 μ high.

Stele—Slightly elliptical, from 3450 to 3750 μ in diameter, with irregular-shaped pith from 1050 to 1125 μ in diameter; the pericycle 1 to 2 cells wide, not well defined; vessels, phloem, fibers and parenchyma lying between pith and pericycle. Pericycle parenchymatous; the cells thin walled, in cross-section hexagonal, radially shortened, mostly about 28 to 52.5 μ ; in longitudinal section oblong, from 30 to 60 μ high. Vessels in cross-section oval, long axis radial, not adjacent to other vessels except in peripheral rows, but grouped to form a band 2 to 3 vessels deep, with larger vessels toward the pith; radial diameter of large vessels from 480 to 600 μ , tangential diameter from 315 to 375 μ , the walls 3 to 4 μ thick; radial diameter of pores in peripheral ring from 15 to 270 μ , tangential diameter from 45 to 135 μ ; smallest vessels near the periphery of the stele often adjacent, irregular in shape with greatest diameter tangential. Vessel perforations simple. Character of pitting of vessel walls not visible. Tyloses present in some of the vessels. Phloem groups about 60 μ in diameter; the cells hexagonal, thin walled, from 7 to 35 μ in diameter; between vessels of the peripheral row. Parenchyma cells immediately surrounding vessels elongate-hexagonal in cross-section, mostly about 14 by 52.5 μ , thin walled. Fibers in cross-section mostly hexagonal, from 14 to 35 μ in diameter, the walls about 7 μ thick with conspicuous simple pits. Length not determinable; ends pointed. Parenchyma cells of pith round to hexagonal in cross-section, from 31.5 to 56 μ in diameter, mostly approaching the larger diameter.

Reports of fossil palm roots are far fewer than those of fossil palm stems. Stenzel¹ describes 62 species of fossil palm woods as contrasted with 4 species of palm roots. Of the species described by him, *P. angiorhizon* and *P. astron radiculatum* are from the Upper Cretaceous of Mexico. A third North American species, *P. anchorus* from the Cretaceous of New Jersey, has been described by Stevens.² The Pliocene species differs from all of these in character of stele or cortex or both.

Drabble³ has published descriptions of a number of modern palm roots, but none of the species described by him is identical with that of the fossil species under consideration. This specimen was compared with a number of roots of the modern *Washingtonia*. These were found to vary considerably in size, in proportion of cortex to stele and in the amount of pith present. A root about 6.75 μ in diameter with a stele about 3 mm. in diameter resembled the fossil more closely than the others examined. The general arrangement of tissues in the fossil and modern specimens was found to be the same; the chief difference between the two being the size and number of vessels present and the character of the phloem groups. The vessels of

¹ Stenzel, K. G., Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, Band 16, Heft 4, 1-182, 1904.

² Stevens, Neil E., Amer. Jour. Sci., Ser. 4, vol. 34, 421-436, 1912.

³ Drabble, Eric, Trans. Linn. Soc., Ser. 2 Bot., vol. 6, 427-487, 1905.

the modern root were found to be considerably smaller and more numerous than those of the fossil, while the phloem groups in the modern specimen were found to be more numerous, larger and more regular in shape than those in the fossil specimen. Since the Pliocene palm root differs somewhat from that of *Washingtonia*, and since it was associated with palm stems that differ rather markedly from those of *Washingtonia*, it is referred to *Palmoxylon mohavensis*, the species of palm represented by wood in the deposits.

Collection—Univ. Calif. Coll. Pal. Bot., Types, Nos. 154, 155; slides 154, 155 A-B.

Pinus kelloggi new species

(Plate 1, figs. 1-3)

Transverse Section—Growth rings easily distinguished; false rings from 90 to 240 μ wide; normal growth rings from 375 to 2000 μ , average width of 45 rings including false rings 489.40 μ . Transition from early to late wood abrupt, the late wood in normal growth rings forming one-fourth to one-half of the ring. Early wood tracheids mostly square, the walls rather thick, radial diameter from 17.5 to 28 μ , tangential diameter from 17.5 to 24.5 μ . Late wood tracheids with very thick walls, radial diameter from 7 to 17.5 μ , tangential diameter from 17.5 to 24.5 μ . Medullary rays rather inconspicuous, distant 2 to 10 rows of tracheids. Resin ducts numerous and conspicuous, mostly in the late wood: maximum diameter from 105 to 157.5 μ ; the epithelium composed of several layers of cells, the cells variable in shape, mostly thin walled; tyloses present.

Radial Section—Wood tracheids with bordered pits in one row, the tangential walls of the summer wood pitted. Ray tracheids numerous, chiefly marginal, occasionally interspersed; thin walled, not dentate, commonly contracted at the ends, from 38 to 70 μ long. Ray parenchyma cells thick walled, from 42 to 77 μ long, often somewhat contracted at the ends, the end walls commonly oblique; the upper, lower and end walls with numerous pits, the lateral walls with 1 to 4 oval, half-bordered pits per cross-field.

Tangential Section—Fusiform rays from 180 to 420 μ high and 28 to 70 μ wide; the cells of the inflated portion thin walled, round, oval or irregular in shape, from 7 to 21 μ in diameter, the resin duct of medium size; the terminals equal or nearly so, the cells thick walled, round to oval, 7 to 24 μ maximum diameter. Ordinary rays uniseriate or biseriate in part, from 1 to 18 cells high; the cells variable from round to oval, maximum diameter from 7 to 21 μ , variability in size and shape of cells more conspicuous in the biseriate rays.

Three of the species of *Pinus* existing on the American continent today possess wood with thin smooth-walled ray tracheids, and thick-walled ray parenchyma cells with small half-bordered pits on their lateral walls. These species are *P. cembroides* Zucc. and its varieties, *P. cembroides monophylla* Voss, *P. cembroides edulis* Voss and *P. cembroides parryana* Voss, *P. balfouriana* Murray and *P. aristata* Engelm. Owing to similarity in structure of the wood of these species, and to individual variation within a species, it is practically impossible to positively identify a given wood specimen of one of these species on the basis of structure alone. However, environmental conditions indicated by the other species of the Ricardo assemblage would be favorable for *P. cembroides* or its varieties, and unfavorable for *P. balfouriana* or *P. aristata*. Hence histological data together with ecologi-

cal data indicate that *P. cembroides* is the modern equivalent of the species represented.

No pines of this type have previously been recorded from the Pliocene of California. Dorf has described two species of *Pinus* of this age in the state, one of which resembles the modern *P. sabiniana*, the other *P. muricata*.

Pinus kelloggii is named in honor of Miss Louise Kellogg, who assisted in making some of the early collections from the locality.

Collection—Univ. Calif. Coll. Pal. Bot., Type, No. 156; slides 156 A-C.

Cupressus sp.

(Plate 2, figs. 1-3)

Transverse Section—Growth rings fairly uniform, from 1200 to 1500 μ wide, but originally wider as a large part of the spring wood is considerably compressed and distorted in most of the growth rings. In an unsectioned specimen growth rings rather irregular in outline from 0.5 to 1.0 mm. wide. Tracheids in spring wood mostly rounded, some square, radial diameter 45.5 to 73.5 μ , tangential diameter 45.5 to 73.5 μ . Transition from early to late wood rather abrupt. Late wood forming a narrow band about 5 cells wide. The tracheids oval to oblong, radial diameter 17.5 to 28 μ , the walls but slightly thicker than those of the spring wood. Rays numerous, conspicuous, distant 1 to 6 rows of tracheids. Resin cells few, scattered throughout the growth ring.

Radial Section—Wood tracheids with bordered pits in one row; the pits elliptical, long axis horizontal, about 12.2 by 14 μ including border, the orifice about 3.5 by 5 μ . Rays without tracheids, mostly somewhat resinous. Ray cells from 87.5 to 122.5 μ long, the end walls vertical or oblique. The upper, lower and end walls mostly thin, without conspicuous pits. The lateral walls with 2 or 3 oblique, elliptical half-bordered pits per cross-field; the pits about 6 by 4 μ , the border rather narrow. Character of pitting on the tangential walls of the late wood tracheids not visible. Resin cells from 17.5 to 21 μ wide, about 87.5 μ high.

Tangential Section—Rays uniseriate, rarely biseriate in part, from 3 to 25 cells high, averaging from 12 to 15. The cells chiefly elliptical with long axis horizontal or round, or where biseriate and rarely elsewhere, elliptical with long axis vertical from 14 to 31.5 μ high and from 17.5 to 28 μ wide.

Because of the difficulty in distinguishing between species of this genus, even when all histological features are visible, the distortion of the growth rings and partial obliteration of the pitting in the fossil specimen makes accurate determination of the species practically impossible. The various species of *Cupressus* are localized in their distribution at the present time. *C. nevadensis* Abrams now grows nearer to Last Chance Gulch than any other species. This fact, together with ecological data discussed later, suggests that *C. nevadensis* may be the species represented. However, the possibility that it may be *C. forbesii* Jepson or *C. arizonica* Greene should not be overlooked. The physical conditions under which these species now grow are quite similar. *C. forbesii* and *C. arizonica* occur at greater distances from Last Chance Gulch than does *C. nevadensis*; however, they are more nearly associated with the modern equivalents of the Ricardo species than is *C. nevadensis*.

Cupressus has not previously been recorded from the Pliocene of California. It is represented by several modern species in the Pleistocene floras of the state.

Collection—Univ. Calif. Coll. Pal. Bot., No. 157; slides 157 A-C.

Quercus ricardensis

(Plate 3, figs. 1-3)

Transverse Section—Diffuse-porous; the growth rings fairly regular in outline, variable in width from 375 to 1200 μ , marked by a narrow band of radially shortened wood fibers in the late wood and slightly larger vessels in the spring wood. Pores arranged in radial lines, a single pore wide and continuous from one growth ring to the next, or in radially elongated fan-shaped groups, one pore wide in the early wood and 3 pores wide in the late wood. Pores mostly occurring singly, elliptical with elongated radial axis, or round; occasionally in groups of 2 to 4 when somewhat angular; radial diameter from 24.5 to 112 μ , tangential diameter from 21 to 77 μ ; the walls from 7 to 10.5 μ thick; vessels generally largest in the early wood. Wood parenchyma abundant, forming short irregular, tangential bands, the cells chiefly oval, some round or hexagonal, from 7 by 10.5 μ to 14 by 24.5 μ in diameter, thin walled; occasionally surrounding the larger vessels. Tracheids chiefly in vicinity of vessels; square to hexagonal, from 17.5 to 24.5 μ in diameter, the walls about 3.5 μ thick. Wood fibers round, square, oblong or irregular in shape, from 7 to 14 μ in diameter, the walls 3 to 3.5 μ thick. Rays numerous and conspicuous, mostly narrow, distant 15 to 75 μ .

Radial Section—Vessels with simple perforations, the vessel segments from 30 to 150 μ high, the walls with numerous bordered pits; the pits horizontally elongate-elliptical, about 3.5 by 5 μ including the border, the orifice lenticular. Wood parenchyma cells in vertical series, oblong excepting terminal cells which are conical, mostly about 17.5 μ wide; the walls with simple elliptical pits about 2 by 3.5 μ . Rays homogeneous. The cells oblong, long axis radial, from 21 to 53 μ long; end walls mostly oblique, thick, with numerous conspicuous simple pits; upper and lower walls thick, conspicuously pitted with numerous simple pits; lateral walls with simple or half-bordered elliptical pits about 3.5 μ long.

Tangential Section—Rays predominantly uniseriate and from 3 to 22 cells high; the cells mostly vertically oblong or oval, about 10.5 by 14 μ in diameter. Aggregate rays about 375 to 450 μ wide and 6000 to 12,000 μ high; the cells hexagonal, from 7 to 24.5 μ in diameter. Tracheids 225 to 550 μ long, mostly approaching the shorter limit, considerably curved, the ends taper pointed, walls with bordered pits in one row; the pits about 4 μ in diameter with elliptical orifice. Wood fibers generally somewhat curved, the ends taper pointed, length not determinable.

The structure of this wood clearly indicates that it is of the live oak group. Although of finer texture than the wood of modern *Quercus agrifolia*, as described by Sudworth and Mell,¹ it possesses all of the distinguishing characteristics of this wood. Fossil wood of *Quercus agrifolia* from the Rancho La Brea deposits as described by Frost² is not essentially different from the Pliocene wood.

Several species of *Quercus* have been described by Dorf from the Pliocene of California. Of these *Q. lakevillensis*³ is represented by leaves of the *agrifolia* type, and it is probable that the Ricardo wood might be correctly referred to *Q. lakevillensis*. Since there are no leaves in the deposits, a

¹ Sudworth, G. B., and C. D. Mell, U. S. Forest Service Bull. 75, 1911.

² Frost, Frederick H., Univ. Calif. Pub. Bot., vol. 14, No. 3, 73-98, 1927.

³ Dorf, Erling, Carnegie Inst. Wash. Pub. No. 412, 82, 1930.

more conservative course is followed by assigning a distinct specific name to this wood.

Collection—Univ. Calif. Coll. Pal. Bot., Type, No. 158; slides 158 A-C.

***Robinia alexanderi* new species**

(Plate 4, figs. 1-3)

The wood specimens representing this species are quite variable, but the variations form a series of such a nature as to indicate the presence of but one species. Diversities in the structure of the wood are closely correlated with differences in width of annual rings. Two specimens were selected for sectioning: one with very narrow and one with moderately wide growth rings. The description of microscopic features given below includes the range of variation found in both types of wood. Macroscopic characteristics are based on unsectioned material as well.

Transverse Section—Ring-porous, annual rings from 0.5 to 6.5 mm. wide, the annual rings of a given specimen fairly uniform or variable; narrow growth rings largely early wood; wide growth rings mostly late wood. Vessels in early wood in 3 to 5 rows; occurring (1) singly when round to oval with radial diameter from 60 to 270 μ or (2) in groups when somewhat angular with radial diameter from 30 to 270 μ in diameter; the vessel walls about 6 μ thick. Vessels in late wood rather few, round, oval or angular, with radial diameter from 40 to 105 μ , tangential diameter from 30 to 60 μ ; grouped with tracheids and wood parenchyma to form irregular diagonal to tangential bands from 75 to 270 μ wide. Tracheids in vicinity of vessels in early wood and late wood; mostly angular (square, hexagonal or oblong) largest diameter from 17.5 to 52.2 μ , the walls about 6 μ thick. Wood fibers scattered in groups throughout the growth ring, but rather rare in early wood and forming bands from 90 to 600 μ wide between the bands containing vessels in the late wood; mostly round-hexagonal, from 7 to 28 μ in diameter, the large fibers surrounded by small ones, the walls 7 to 10.5 μ thick. Parenchyma surrounding vessels and connecting groups of pores in the late wood; the cells angular, often with unequal diameters. Rays conspicuous, distant 35 to 255 μ .

Radial Section—Vessels with simple perforations which are often sub-terminal. Vessel walls with numerous bordered pits, which appear to be punctate. The pits horizontally elongate, elliptical, about 7 by 5 to 5.5 μ including the border, the orifice slit-like or lenticular. Large vessels mostly filled with tyloses. Small vessels with spirally thickened walls. Rays homogeneous to heterogeneous. Ray cells varying from horizontally elongate-oblong (about 105 by 24.5 μ), square (about 35 μ) to vertically elongate-oblong (35 by 42 μ). The square and vertically oblong cells often marginal, but not constantly so. The upper, lower and end walls rather thin with few simple pits, or fairly thick and with numerous pits. Lateral walls with inconspicuous simple or half-bordered pits except when in contact with vessels; where half-bordered pits are up to 14 μ long, the border very narrow.

Tangential Section—Rays mostly multiseriate, occasionally uniseriate. Multiseriate rays from 2 to 5 cells wide and 5 to 56 cells high; often irregular in outline, being constricted near the middle or toward either end, occasionally with a uniseriate terminal up to 7 cells high. The cells (1) fairly thick walled, mostly round, from 10 to 21 μ in diameter or (2) rather thin walled and variable in size and shape from round-hexagonal or square with diameter

from 14 to 35 μ , to oblong or vertically elongate-hexagonal and about 38.5 by 17.5 μ to 52.5 by 17.5 μ , the larger cells commonly in the outer row of the ray, the terminal cells small or large. Uniseriate rays 2 to 8 cells high the cells mostly oval from 24.5 to 42 μ high by 21 to 24.5 μ wide. Wood parenchyma cells in vertical rows one cell wide and 4 to 5 cells high; the central cells vertically oblong, 17.5 to 52.5 μ high by 17.5 to 24.5 μ wide; the terminal cells conical, about 42 to 59.5 μ high, the walls with numerous simple pits. Tracheids about 175 to 192.5 μ high, the ends pointed, the walls with spiral thickening and numerous bordered pits; the pits horizontally elongate-elliptical, about 7 by 5 μ , including border, the orifice slit-like. Wood fibers with pointed ends; length and character of pitting not determinable.

The woods of *Robinia pseudoacacia* L. and *Toxylon pomiferum* Rafn. are so closely similar in structure that they have until recently been regarded as indistinguishable in the fossil state. Unpublished studies by I. W. Bailey and Lyman H. Daugherty indicate (1) that punctate pits are present on the vessel walls of *Robinia* and not on the vessel walls of *Toxylon*, (2) that the wood fibers of *Robinia* differ from those of *Toxylon* in having their central portions swollen. As seen in transverse section, these fibers show two distinct diameters, the larger representing those which the section cuts in the swollen central portion, the smaller those at the ends. In contrast, the fibers of *Toxylon* show graded variations in size. As stated above, the fibers of the wood under consideration are of two distinct diameters and punctate pits appear to be present, although the latter can not be proven. It is therefore possible to refer the Ricardo wood to the genus *Robinia*.

Leaves or pods of *Robinia* have been recorded from the eastern United States in beds ranging in age from Cretaceous to Pleistocene. This is the first record of the genus in western America.

Robinia alexanderi is named in honor of Miss Annie M. Alexander, whose early collections in this region have added materially to this paper.

Collection—Univ. Calif. Coll. Pal. Bot., Type, No. 159; slides, 159 A-C.

Undetermined Dicotyledon

(Plate 5, figs. 1-3)

Transverse Section—Diffuse-porous, annual rings from 1 to 2 mm. wide. Pores occurring singly when round to oval and from 75 to 225 μ in diameter, or in groups when more or less angular and from 30 to 225 μ in diameter; rather evenly distributed throughout the growth ring; somewhat larger in the early wood. Wood parenchyma paratracheal. Tracheids abundant. Rays rather inconspicuous, distant 20 to 270 μ .

Radial Section—Vessel perforations simple. Vessel walls with numerous horizontally elongate-oval to hexagonal-bordered pits about 6 by 4 μ including border; the orifice slit-like or lenticular. Walls of small vessels with spiral thickening. Rays homogeneous; the cells horizontally elongate-oblong, from 45 to 75 μ long; the upper, lower and end walls with rather few simple pits; the lateral walls with simple or half-bordered pits; the pits inconspicuous except where rays are in contact with vessels. Wood parenchyma cells vertically elongate-oblong, from 45.5 to 87.5 μ high, the walls with simple pits; the pits few, mostly oval, quite variable in size.

Tangential Section—Rays of two kinds: (1) Uniseriate, from 2 to 18 cells high and (2) multiseriate, from 2 to 5 cells wide, but rarely more than

three cells and frequently uniseriate in large part; from 5 to 32 cells high. The cells thin walled, vertically elongate-oval, from 10.5 to 35 μ high and 8.7 to 21 μ wide, or round and from 5 to 17.5 μ in diameter. Tracheids with pointed ends, about 14 to 17.5 μ wide and 240 to 270 μ high, the walls with broadly oval-bordered pits about 4.5 μ in diameter including border, the orifice slit-like.

Of the numerous modern species of diffuse-porous dicotyledonous wood with which this species was compared, it most closely resembles *Xanthoxylum*, suggesting that it may represent a member of the Rutaceæ.

Collection—Univ. Calif. Coll. Pal. Bot., No. 160; slides 160 A-C.

Descriptions of Fungi in the Wood

(Plate 4, fig. 4; plate 5, fig. 4)

Fungi are abundantly represented by hyphæ and spores in a piece of bark, by numerous hyphæ in the wood of *Pinus*, and by fruiting bodies in *Palmoxylon*. Fungus hyphæ also occur sparingly in the tyloses of *Robinia*, and in one specimen of *Cupressus* wood. While no hyphæ were observed in another specimen of the wood of *Cupressus*, its badly eroded and striated walls indicate that it had been attacked by fungi.

More than one species of fungus is undoubtedly represented in the bark. The hyphæ are abundant, branched, septate, and from 1.5 to 10 μ thick. Several types of spores are present. Spherical fruiting bodies, possibly oogonia, about 38.5 μ in diameter are quite common. Numerous spherical spores about 3.5 μ in diameter are present. Conidia 7 to 14 μ in diameter are fairly common.

The fungus fruiting bodies in *Palmoxylon* are of particular interest. Fungus hyphæ have been reported by Stevens¹ in *Palmoxylon anchorus*, *P. cheyennense*, and *P. cannoni*. Berry² has described spores and hyphæ of *Cladosporites oligocenicum* and *Peronosporoides palmi* in *Palmoxylon cellulolum*. Hyphæ are not abundant in the wood of *P. mohavensis*. Sub-spherical bodies about 42 μ in diameter, apparently borne terminally on hyphæ which are poorly preserved, are visible in the wood. These are comparable to the oogonia of *Peronosporoides* and probably should be referred to this genus. While Berry found numerous hyphæ of *P. palmi* in *Palmoxylon cellulolum*, the scarcity of hyphæ in the Pliocene wood can not be taken as an indication that a different type of fungus is represented, as the fruiting bodies of the Oomycetes often persist long after their hyphæ have disintegrated.

A distinct type of sporangium is abundant in hypertrophied parenchyma cells in the cortex of the palm root. The sporangia are brown spherical bodies 10.5 to 24.5 μ in diameter, or oval in outline and up to 59.5 μ long. They have a variable number of short, filamentous appendages about 1.5 μ in diameter. In one case, several oval spores about 3 μ long are in close proximity to a partially collapsed sporangium. Such fruiting bodies are characteristic of the Chytridiales, of which a number of the Sinychtriaceæ are parasites of angiosperms. It is significant that host plants in wet places are most apt to be attacked by such organisms.

¹Stevens, N. E., Amer. Jour. Sci., Ser. 4, vol. 34, 421-436, 1912; Ser. 5, vol. 1, 431-443, 1921.

²Berry, E. W., Mycologia, vol. 8, 73-79, 1916.

ECOLOGICAL CONSIDERATIONS

In drawing conclusions from fossil wood as to the environmental conditions of the woody plants represented, the species present and the character of their growth rings must be considered. In the case of species which have existed practically unchanged from past geologic ages until the present time, the conditions of habitat under which the species now exist is a clue to the conditions under which they previously existed. In the case of extinct species their nearest living relatives are the best available index. Since conditions which now favor or check development of a species may be assumed to have had the same effect upon its development in the past, and since such conditions are often reflected by growth rings, they may be an important source of information regarding the environmental conditions of fossil woody plants.

Of the woody species from Last Chance Gulch, one is a monocotyledon and hence without growth rings; two are gymnosperms, with well-marked growth rings, and three are dicotyledons with growth rings. The observed variations in width of growth rings of the different species is given in the following table:

TABLE 2—Variation in width of growth rings of the species present

Species	Minimum width	Maximum width	Mean width
Cupressus sp.....	0.500 mm.	1.5+mm.	1.05 mm.
Pinus kelloggi.....	0.090	2.00	0.49
Quercus ricardensis.....	0.375	1.20	1.00
Robinia alexanderi.....	0.450	6.50	2.22
Undetermined dicotyledon.....	1.000	2.00	1.20

From the above table it may be seen that the greatest mean width and maximum width of growth rings is found in *Robinia*, suggesting that this species made the most rapid growth. The mean widths of the annual rings of all species and the minimum width of growth rings of the most rapidly growing species, *Robinia*, signify that growth in general was rather slow. However, occasional rapid growth is indicated by the maximum width of growth rings found in *Robinia*. The data in table 3 show that most of the specimens exhibit only narrow or wide growth rings near the center of the stems, although both types are present in some specimens. Since age of the stem apparently had little effect in determining the width of growth rings within this species, such variations as are observed may be attributed

to different environmental conditions. The relative importance of the various ecological factors involved in causing variation in rate of growth can be determined only after considering the habitats of the species represented, as judged by the habitats of modern related species.

TABLE 3—Variation in width of growth rings in *Robinia*

Specimen number	No. of rings	Minimum width	Maximum width	Mean width	Center of stem present
8E	18	0.45 mm.	0.75 mm.	0.68 mm.	
11	7	0.50	1.00	0.78	×
9	25	1.00	1.50	1.08	
7	7	1.00	2.00	1.50	×
5	14	1.00	3.50	1.78	×
6	14	1.00	2.50	1.85	×
10C	9	2.00	3.50	2.61	
3	4	2.50	4.50	3.37	×
2	8	2.50	4.00	3.62	
1	15	3.00	4.50	3.86	
4	12	5.00	6.50	5.62	

According to Sudworth,¹ *Pinus cembroides*, the living species most closely similar to *P. kelloggi*, ranges from southeastern Arizona and southern New Mexico to southern Mexico and southern Lower California. *P. cembroides edulis* is distributed from western Texas through New Mexico, western Colorado, eastern and southwestern Utah, northern and eastern Arizona, northern Mexico and northern Lower California. *P. cembroides monophylla* is found from southern Idaho, eastern Utah and northern Arizona through Nevada to the eastern slope of the southern Sierra Nevada and thence into southern California and northern Lower California. *P. cembroides parryana* ranges southward from the San Jacinto Mountains in southern California to the southern end of the San Pedro Martir Range in Lower California. Throughout its range, the species including its varieties grows on dry foothills, mesas, mountain slopes, and precipitous canyon sides in poor, shallow, rocky or gravelly soil often in the crevices of rocks. It is restricted to the Sonoran Zones.

According to Jepson,² seven species of *Cupressus*, all of which are of localized occurrence, grow in California at the present time. *Cupressus macrocarpa*, *C. goveniana*, and *C. pygmaea* are maritime or coastal species of the Transition Zone. *C. sargentii* and *C. macnabiana* are

¹Sudworth, G. B., U. S. D. A. Bull. 460, Maps 5, 6, 7, 1917; U. S. D. A. Forest Service, page 33, 1908.

²Jepson, W. L., *A Manual of the Flowering Plants of California*, 1925.

found in both the Transition and Upper Sonoran Zones. The former is found from the Santa Cruz Mountains to Mount Tamalpais, in Hoods Peak Range and Mendocino County on dry mountain slopes in more or less isolated groves. *C. macnabiana* inhabits dry hillsides and canyons from Napa County to Shasta County and thence east to the Sierra foothills and as far south as Yuba County. *C. forbesii* and *C. nevadensis* are restricted to the Upper Sonoran Zone, *C. forbesii* being found on dry mountain slopes of Orange County, San Diego County and Lower California, while *C. nevadensis* is local on Piute Mountain, Kern County. The occurrence of *C. arizonica* var. *bonita* Lemm. at altitudes of 4000 to 7000 feet on the Santa Rita and Santa Catalina Mountains of Arizona is also noteworthy.

Since *Washingtonia filifera* is the only native palm found in California at the present time, the conditions under which it grows may be considered to approximate the environmental conditions of the fossil species. According to Jepson,¹ *Washingtonia filifera* grows on the northwestern and western margins of the Colorado Desert and thence southward to Lower California. Since it requires an abundant root supply of moisture, it is highly localized in its distribution, occurring only near streams or springs. It inhabits wet or moist, sandy, often rocky and alkali soil, from near sea-level to 3500 feet. It appears to be tolerant of shade in youth, but later grows in full strong light, occurring widely scattered or forming open pure stands. The region in which it is found is characterized by long dry summers and often limited winter precipitation.

Of the ten species of evergreen oaks occurring in California at the present time, three are confined to northern California and one, *Q. tomentella*, is insular. Of the six species indigenous to the mainland of southern California, *Q. dumosa* and *Q. palmeri* are strictly shrubs. The species attaining tree size in southern California are *Q. chrysolepis*, *Q. agrifolia*, *Q. engelmannii* and *Q. wislizenii*. *Q. chrysolepis* has a greater range and occurs under more varied conditions than any of the other species. Except in the foothills, it is indigenous practically throughout California and also occurs in southern Oregon, the mountains of northern Lower California, Sonora and Arizona. *Q. agrifolia* is of larger size and more general distribution than any of the other species in southern California. It grows on valley floors, rocky hills, steep canyon sides and dry mesas, forming pure open forests or at times in mixture with *Q. chrysolepis*, *Q. engelmannii* or *Q. wislizenii*. It is distributed in the Transition and Upper Sonoran Zones of the Coast Ranges from Lower California to northern Sonora and Napa Counties. *Q. engelmannii* is restricted to southern California and

¹ Jepson, W. L., *Trees of California*, 1923.

Lower California, where it occurs in a zone 15 to 40 miles back of the coast. It usually grows in association with *Q. agrifolia* on hill slopes and mesas. *Q. wislizenii* is distributed on hill slopes and valleys in the Coast Ranges from Lower California to Shasta County and is also present in the Great Valley and Sierra Nevada foothills at elevations of 200 to 5000 feet.

Of the four aborescent species of *Robinia* occurring in North America, *R. neo-mexicana* Gray is found within the shortest distance to the Ricardo beds. It extends from the mountains of northern Sonora through the Santa Rita and Santa Catalina mountains of Arizona at elevations of 4000 to 7000 feet, through northern New Mexico to the valley of the Purgatory River in Colorado and into Utah where it occurs at Kanab and in Mount Zion Canyon. In typical form it is a low shrub, never attaining the size of trees represented in the Ricardo beds. The maximum reported size of the variety *luxurians* Dieck. is 25 feet in height and 8 inches in trunk diameter. The trunks of *R. alexanderi* are comparable in size to those of *R. pseudoacacia* L. which is not known to be indigenous west of southern Illinois.

A survey of the present geographic ranges of the modern equivalents of the species represented in the Ricardo flora shows that there is no area where all of these species are now known to occur. However, some of the more widely distributed species are now found within short distances of those which are localized. *Pinus cembroides edulis* and *P. cembroides monophylla* are distributed throughout the range of *Robinia neo-mexicana*. Both *Robinia neo-mexicana* and *Cupressus arizonica* have been reported at elevations of 4000 to 7000 feet on the Santa Rita and Santa Catalina Mountains of Arizona. A live oak, *Quercus chrysolepis*, also occurs in the Santa Rita Mountains. With the exception of *Robinia*, all of the determined species are represented by closely related species in California. *Pinus cembroides parryana* grows within short distances of *Cupressus forbesii* and several species of live oak in eastern San Diego County, Cuyamaca Quadrangle and the territory to the east, at an elevation of 3000 feet, near Jacumba Hot Springs. *Cupressus forbesii* has been reported approximately 41 miles northwest of this station at Cedar Canyon between Dulzura and Jamul, about 32 miles to the west on Mount Tecate and approximately 32 miles to the north in the Laguna Mountains. *Quercus engelmannii* occurs on Mount Tecate. *Q. agrifolia* is widespread in San Diego County in the region to the north and west of Campo and extends east as far as Jacumba Hot Springs, where it grows at an elevation of 2822 feet. Both *Q. chrysolepis* and *Q. wislizenii* occur on the Hanson Laguna range at the Mexican boundary.

Another locality at which *Pinus cembroides* grows within short distances of modern equivalents of the species represented in the Ricardo flora is on the eastern slope of the San Jacinto Range between San Jacinto Peak and Santa Rosa Mountain. At the head of Carriso Creek (Indio Special Map T6S, R5E) at an elevation of 3500 feet, *Washingtonia* occurs at Dos Palmos Spring. This locality is about 3 miles northeast of Pinyon Flat which has an elevation of 4000 feet. *Pinus cembroides monophylla* grows here. Approximately 7 miles southwest of Dos Palmos Spring at an elevation of 4549 feet, *Quercus agrifolia* is found at Vandeventer Flat (San Jacinto Quadrangle, T7S, R5E). Sudworth¹ reports that *P. cembroides parryana* occurs near this locality, which is at the head of Palm Canyon and approximately 33 miles south of Palm Springs. At Andreas Canyon, about 8 miles south of Palm Springs, *Washingtonia* grows at an elevation of 800 feet. According to Sudworth, *Pinus cembroides monophylla* occurs in this vicinity at an elevation of 2000 feet. *Q. chrysolepis* and *Q. wislizenii* are common in this region but occur chiefly at higher elevations.

A consideration of the present climatic conditions at the localities in which the greatest number of modern representatives of the Ricardo flora now exist is of importance, since the climate at these localities may be assumed to approximate that which prevailed in the vicinity of Last Chance Gulch during Ricardo time. Reference to C. H. Merriam's Life-Zone Map of the United States² shows that the region in which *Robinia neo-mexicana* is associated with *Pinus cembroides* lies within the Upper Sonoran Zone. The California localities at which several of the modern representatives of the Ricardo flora occur within short distances of one another lie partly within the Upper Sonoran and partly within the Lower Sonoran Zones. C. H. Merriam states that these zones are distinguished by a normal mean temperature of 78.8°F. for the six hottest consecutive weeks and an annual sum of 18,000°F. effective temperature (above 43°F.). Throughout the range of *Robinia neo-mexicana* the approximate annual precipitation varies from 10 to 20 inches. In California at the locality near Campo where annual precipitation is between 10 and 20 inches, and at Dos Palmos where it is less than 10 inches, precipitation is largely winter rainfall. The mean annual rainfall recorded at the Palm Springs weather station at an elevation of 584 feet is 4.13 inches. These data indicate that the annual rainfall received by the Ricardo assemblage was probably less than 20 inches.

¹ Sudworth, G. B., U. S. D. A. Forest Service, page 33, 1908.

² Merriam, C. Hart, Nat. Geog. Mag., vol. 6, 229-238, 3 maps, 1894.

Since available moisture supply in a warm climate is of utmost importance in determining the rate of plant growth, the narrow minimum and mean widths of the growth rings in the fossil woods, note table 2, may also be regarded as an indication that the Ricardo flora grew in a region of rather limited rainfall. Under conditions of high temperature and limited precipitation, the growth rates of species which are able to grow close to the water table are often quite rapid. Since *Robinia* now commonly grows in the vicinity of streams, and since such rapid growth as shown by some of the fossil *Robinia* wood specimens could have been made only where moisture was plentiful, the wide growth rings in some of the fossil wood of this species suggest that these specimens grew near a stream. That *Palmoxylon* was associated with the more rapidly growing specimens of *Robinia* is indicated by the occurrence at one point in the beds of a group of palm roots, apparently representing one tree, within a short distance of standing *Robinia* stumps with wide growth rings. In addition to being associated with the rapidly growing specimens of *Robinia*, the probable occurrence of *Palmoxylon* in close proximity to a stream is indicated by the present restriction of *Washingtonia* to localities near streams or springs and the presence in the fossil palm roots of a parasitic fungus belonging to a group which reproduced by motile spores. Hence the modern habitats of *Robinia* and *Washingtonia* together with the character of the fossil woods of *Robinia* and *Palmoxylon* may be regarded as evidence that a stream was present in the locality during the Ricardo Pliocene.

The presence of a stream in the region characterized by high temperature and low rainfall would furnish the basis for an explanation of the diversity in width of growth rings observed in *Robinia*, note table 3. Under such climatic conditions the rate of growth would be expected to decrease as distance from the stream increased, and differences in growth rate would be most noticeable on a slope rising abruptly from the stream-bed. The presence of some *Robinia* specimens with very narrow growth rings and others with wide growth rings suggests that those which made rapid growth grew near a stream-bank, while the slow-growing trees grew well up on a slope rising rather abruptly from the stream-bed.

The mean widths of the growth rings of the fossil specimens of *Quercus ricardensis*, *Pinus kelloggi* and *Cupressus* sp. indicate that these species made slow growth. Since the growth rate of *Robinia* seems to be correlated with differences in water supply available to the different specimens, it is not unlikely that the slow growth of *Quercus*, *Pinus* and *Cupressus* may be largely attributed to their

having grown at some distance from the water table. Due to inherited tendencies of the species, growth rates of different species may be quite different under a given set of environmental conditions. This makes it difficult to positively establish the relative positions of the various species, since all but *Robinia* and *Palmoxylon* are represented only by small pieces of wood. In view, however, of the low minimum and mean widths of the growth rings of *Pinus*, *Cupressus* and *Quercus*, it may be assumed that they grew well above stream-level and at a point considerably up the valley from the situation occupied by *Robinia* and *Palmoxylon*. This assumption finds support in the present distribution of related species in the San Jacinto Range between San Jacinto Peak and Santa Rosa Mountain. Here, *Washingtonia* is found in the lower stretches of the valleys, with *Pinus cembroides monophylla* and *Quercus agrifolia* occupying successively higher positions, for the most part well above stream-level and toward the heads of the valleys. *Cupressus* does not occur at this locality, but is found in eastern San Diego County where it grows under conditions favorable for the growth of *Quercus agrifolia*. Hence the habitats of the modern equivalents suggest that *Pinus kelloggi*, *Quercus ricardensis* and *Cupressus* sp. grew at a considerably higher elevation than *Palmoxylon* and *Robinia*, and on slopes well above the stream.

The relative abundance of specimens of the various species found in the deposits corresponds to that which would be expected under conditions similar to those suggested above. As already stated, the numerous stumps at the Saltdale Petrified Forest all represent *Robinia*, although *Palmoxylon* roots occur in a position indicating that this species also grew at the locality. The other species are known only from relatively few and comparatively small specimens in the collections. Since chances for deposition of plant fragments are greatly decreased as their distance from a site of deposition is increased, the relative scarcity of *Pinus*, *Cupressus* and *Quercus* in the deposits may be attributed to their having lived on the slopes well upstream. All available evidence indicates that *Palmoxylon* and *Robinia* grew at a comparatively low elevation in close proximity to a stream, with the result that wood of these species has been preserved in comparative abundance.

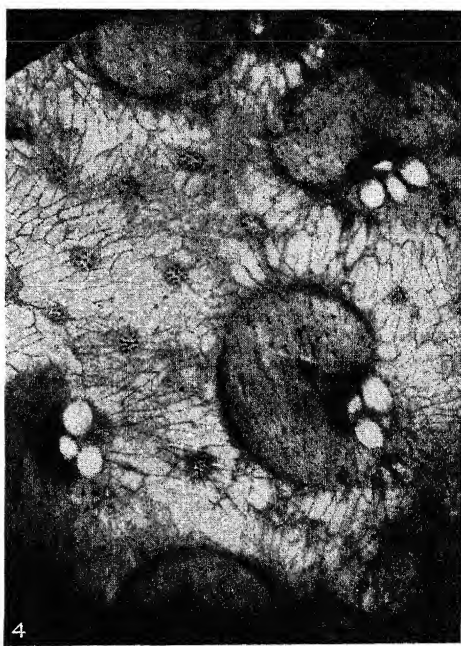
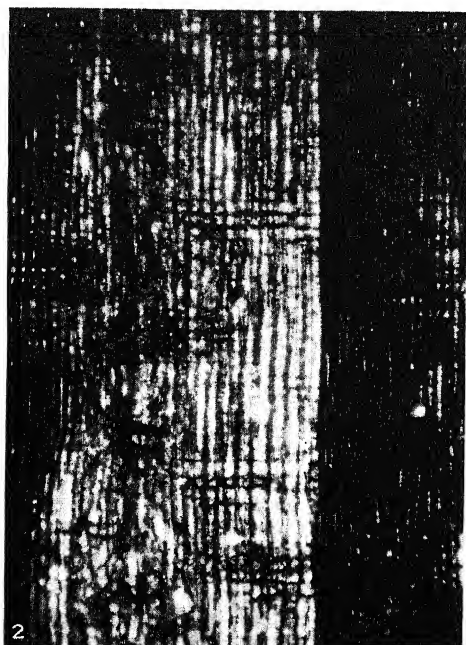
The environmental conditions gained from a study of the Ricardo woods corroborates the evidence derived from an investigation of the fauna and suggests a plains habitat with nearby slopes rising rather abruptly from the stream-banks.

SUMMARY

The remains of woody plants which have been described from the Ricardo Pliocene deposits of Last Chance Gulch consist of well-preserved petrified wood of *Pinus kelloggi* n.sp., *Cupressus* sp., *Palmoxylon mohavensis* n.sp., represented by stem and root fragments, *Quercus ricardensis* n.sp., *Robinia alexanderi* n.sp., and an undetermined dicotyledon. Fungi, represented by hyphæ and spores in a piece of bark, by hyphæ in the wood of *Pinus*, *Cupressus* and *Robinia*, and by fruiting bodies in a palm root have also been found. The specimens were associated with mammalian remains which have been referred to the earliest Pliocene. The species represented are all similar to, or possibly identical with, those living now in the southern United States, which is consistent with their reference to the Pliocene. The disparities of their range, as compared to related living species, indicates that sufficient time has elapsed to warrant assigning them to this position near the close of the Tertiary. The present habitats of related trees and the growth rings in the fossil specimens suggest that the Pliocene assemblage grew in a steep-sided valley in a region characterized by low rainfall and temperature approximating that which distinguishes the Upper from the Lower Sonoran Zone. At the present time the closest approach to these environmental conditions is found in the San Jacinto Range between San Jacinto Peak and Santa Rosa Mountain, where palms are found living in the lower stretches, with pines and live oaks occupying the slopes of the upper portions of the valleys. The suggested Pliocene climate differs from the present climate of the Mohave Desert in that the former is characterized by less extreme aridity.

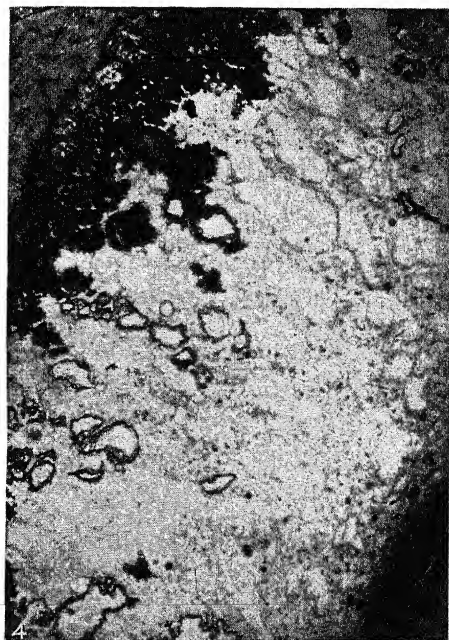
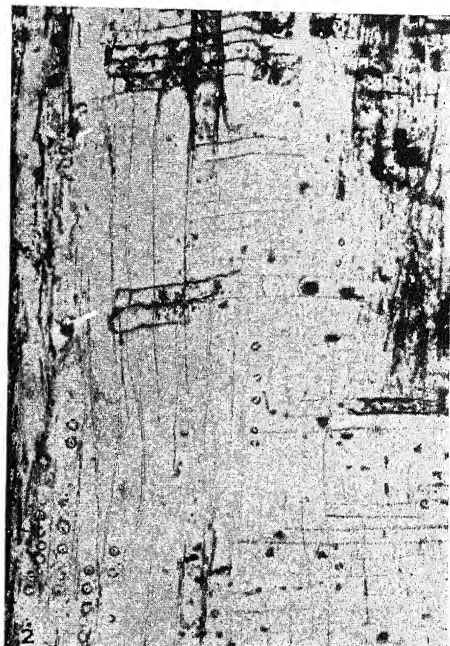
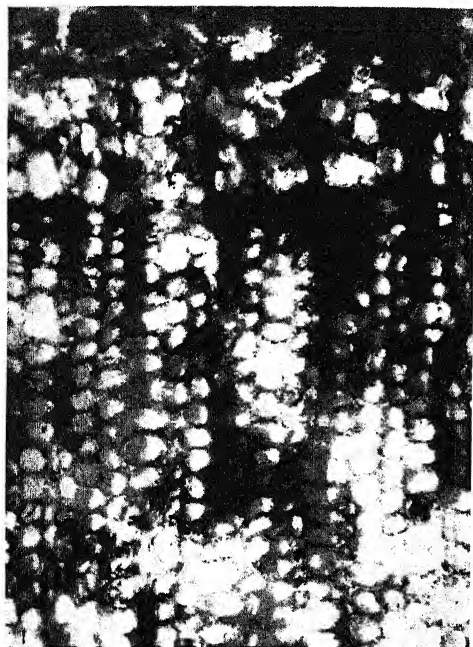
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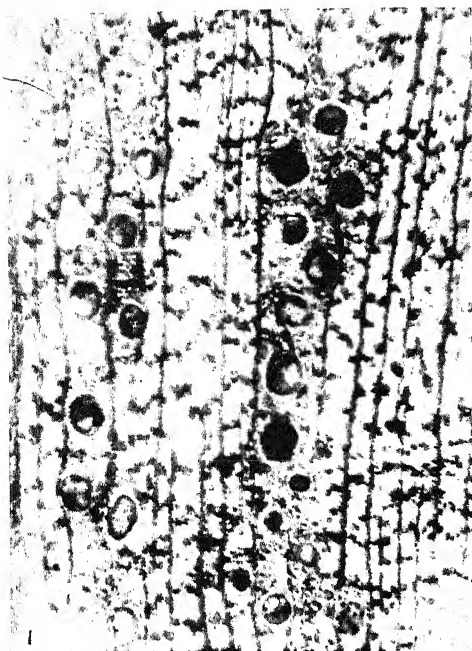
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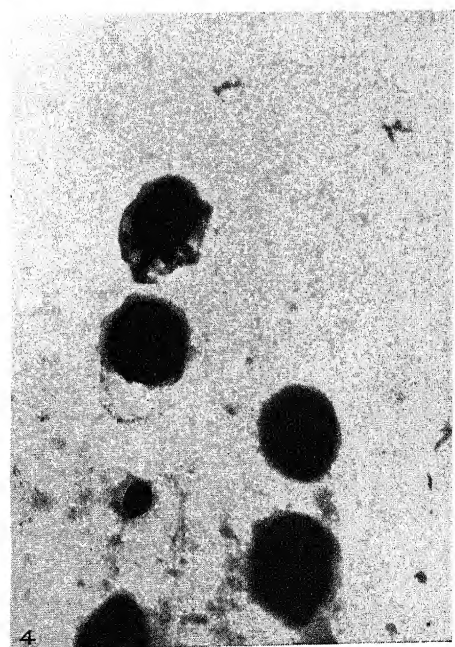
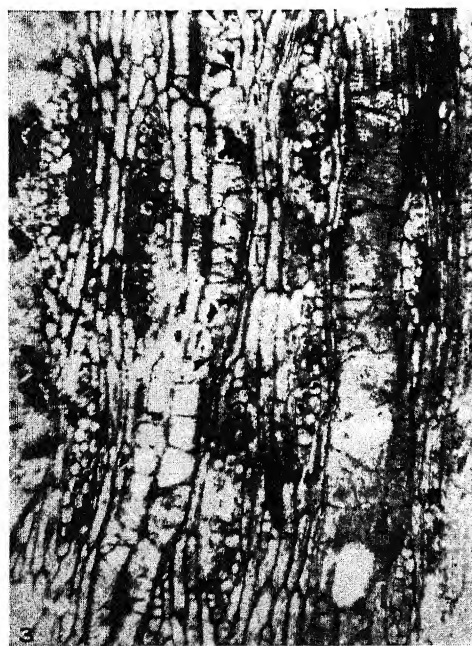
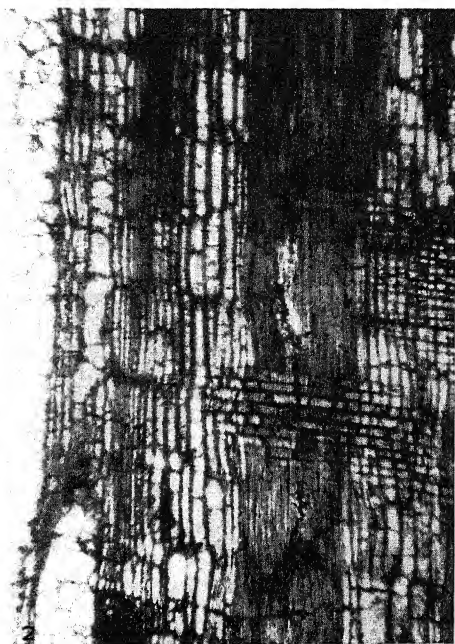
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